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Relationships matter: How the social environment affects individual fitness-related behaviors

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Relationships matter: How the social environment affects individual fitness-related behaviors

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Dana Marie Williams

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ABSTRACT OF THE DISSERATION

Relationships matter: How the social environment affects individual fitness-related behaviors

by

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Doctor of Philosophy in Biology

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Professor Daniel T. Blumstein, Chair

Individual behaviors related to fitness-enhancing events, like foraging and reproduction, are often shaped by internal and external factors. Of these factors, an individuals' social environment has a dynamic effect on their behavior and this is particularly true for different types of social relationships. For example, affiliative interactions can increase an individuals' sense of social security and improve their health, while agonistic interactions can lead to competition that alter an individuals' access to resources. Social network analysis allows for the quantification of an individuals' social relationships to examine whether specific aspects of sociality, such as number of social partners or centrality to a group, affect an individuals' behavior. Social relationships do not have uniform effects across species and social systems and therefore, likely influence fitness-enhancing events in different ways. Here, I examine how an individuals' social environment influences three important behaviors: their personality, how they solve problems, and how they may learn. In Chapter 2, I use bivariate Bayesian models to examine the co-variance between an individuals' social network position in both their affiliative and agonistic networks and two consistent measures of anti-predator behavior: boldness, a measure of risk-taking, and docility, a measure of defensive aggression. I found that docile individuals were less involved in their agonistic network but that docility had no correlation with affiliative behavior. Boldness was not influenced by social environment. Overall, social environment impacts different anti-predator behaviors in different ways and in marmots, aggressive relationships are more important to anti-predator behavior than affiliative ones. In Chapter 3, I used structural equation models to examine how social network position indirectly affects a suite of behaviors used to solve a novel foraging problem. I found that marmots who used a diversity of behaviors were more successful problem-solvers and those who received aggression were less so. Social position indirectly impacted problem-solving success by altering the behaviors used when attempting to solve the box. Individuals who received high aggression were less persistent, less behaviorally diverse and less behaviorally selective. Thus, an individuals' aggressive social environment alters how they approach a novel problem. In Chapter 4, I used generalized linear mixed effects models and network-based diffusion analysis to examine whether individuals learned and whether they socially transmitted foraging information on location or foraging skills. Not all yellow-bellied marmots learned to solve a novel foraging task or became more efficient at solving it with experience. While some colonies did socially transmit information on food location, they rarely socially transmitted motor skills associated with solving the foraging task. Overall, marmots are not extractive foragers and do not need to have the skills to solve complex foraging problems, but like other rodents, attract one another to locations of food. Together, these studies illustrate the value of studying social relationships using modern social network statistics.

The dissertation of Dana Marie Williams is approved.

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2021

DEDICATION

Like many people in the field of behavioral ecology, my story started in a little New England seep looking for liverworts with my grandmother, Nancy Williams, and in wide-eyed enrapture by a National Park Service wildlife biologist in a campground that my parents, Rick Williams and Laurie Pike, brought me to as a child. It has been an incredible privilege to have these individuals in my life encouraging me in my pursuit of a career in biology and their perpetual enthusiasm for my many exploits.

My advisor, Dan Blumstein, guided me through my first research project as an undergraduate at RMBL and aided me in my subsequent travel around the world doing field work even before accepting me into his lab. His mentorship has been invaluable as has been his enthusiasm for my projects (especially when I didn't have any), dinner parties, conversation and opportunities.

My lab mates and friends, particularly Gabriela Pinho, for helping counsel me through the various struggles of graduate school both personal and professional as well as sharing code, editing, advice, adventures and food. My long-term students Catherine Wu, Andrew Evans, and Briana Barr, as well as everyone else who helped work on the project both with the puzzle box study and marmoteer field work (and sometimes both!)- thank you for the hours you sacrificed looking at marmot videos, lugging around heavy puzzle boxes and for tolerating my stumbling mentorship/supervision. I may have written these chapters but you all did a lot of the footwork to get them here.

My additional thanks go to my committee members, Noa Pinter-Wollman, Peter Nonacs, and Greg Grether for their mentorship and feedback for multiple drafts of projects. And a number of journal editors and reviewers who improved these and other manuscripts immensely and whose feedback taught me many things about statistics, writing and people.

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Acknowledgements

I hereby confirm that the contents of this thesis are my own work and all sources quoted, paraphrased or otherwise are properly acknowledged in the references. I confirm that this thesis has not been previously submitted for the awarding of a degree to this or any other university. Any portions of this thesis that resulted from the contributions of others are detailed below or in the Acknowledgements of each respective section.
Chapters 2 to 4 were written as independent manuscripts intended for publication. These chapters were all conducted with co-authors (acknowledged below) but I designed and collected data for each study and the manuscripts were all drafted by myself with advice and supervision by my advisor, Dr. Daniel T. Blumstein. Manuscripts were prepared following the formatting of the respective target journals, outline below, and so there are minor formatting differences between all chapters.

Chapter 2 was prepared for publication in *Proceedings of the Royal Society B: Biological Sciences* and so follows their formatting with the exception of citation style, which follows *Animal Cognition* style to allow for visibility of author names. It was co-authored with Samantha Beckert and Daniel T. Blumstein and included help from Julien G.A. Martin for statistical analysis.

Chapter 3 was published in *Animal Cognition* on 2021 under the title “Social position indirectly influences the behaviors used to solve problems”. Contributions by my co-authors, Catherine Wu and Daniel T. Blumstein, are outlined in the contribution section.

Chapter 4 was prepared for publication in *Animal Cognition*. It was co-authored with Andrew Evans, Briana Barr and Daniel T. Blumstein.

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Williams DM, Wu C, Blumstein DT. 2021. Social position indirectly influences the traits yellow-bellied marmots use to solve problems. Ani. Cog. 24: 829-842.

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PRESENTATIONS

Williams DM (presenter), Wu C, Blumstein DT. Indirect influence of sociality on innovation in yellow-bellied marmots. Animal Behavior Society 2019. Chicago, IL, USA. July 23-27, 2019. Oral presentation.

Williams DM (presenter), Barr B, Evans AW, Blumstein DT. Social learning in yellow-bellied marmots (*Marmota flaviventer*). Animal Behavior Society 2020. Online. July 28-31, 2020.

Williams DM (co-presenter), Beckert S (co-presenter), Martin JGA, Blumstein DT. Social environment and anti-predator personality traits. Animal Behavior Society 2021. Online. August 3-6, 2021.

Chapter 1: General Introduction

Social groups provide protection from predators, aid in finding mates, allow for collective resource defense and for ecological 'shortcuts' such as social learning and the formation of culture. However, group living also comes with costs such as disease transmission and competition that create a cost-benefit trade-off for when and how much individuals should invest in social relationships (Ward and Webster 2016). This trade-off makes an individuals' social environment highly influential in shaping their behavior. While group size and density have strong effects on fitness, including increased predator protection (Caro 2005) or by increased competition for food (Pulliam 1984), the specific types of relationships an individual engages in can also shape their behavior (Wey et al. 2008; Krause et al. 2010). For example, affiliative relationship strength (Blumstein et al. 2017; Nadler et al. 2021) explains variation in anti-predator behavior, improves health outcomes (Umberson and Monetz 2011), longevity (Silk et al. 2010; Brent et al. 2017), and reproductive success (Vander Wal et al. 2015). Social aggression and exclusion from resources make individuals more likely to take risks (Goss-Custard 1980; Giraldeau and Caraco 2018) and bolder individuals are often more socially aggressive (Sih et al. 2004; Bell 2007). Additionally, subordinate individuals may invest in social relationships in order to earn tolerance from dominants while foraging (Marshall et al. 2015). Thus, social relationships should be included when examining factors that explain variation in individual behavior.

Social networks are used to quantify an individual's relationships and can extract information on specific aspects of an individuals' relationships including how many and how often individuals interact with conspecifics and how often they move between different social cliques in their groups (Wey et al. 2008). Networks, and thus the relationships examined, can either be weighted, taking into account the number of times an interaction has occurred or unweight, where interactions are measured as binary (0/1) did these individuals interact. Networks can also be directional, taking into account initiated (out) interactions or received (in) interactions.

Common social network measures include: degree (in and out), strength (in and out), closeness (in and out), betweenness centrality, eigenvector centrality, negative average shortest path length, and clustering coefficient (local and global). Degree, strength, eigenvector centrality, negative average shortest path, and the clustering coefficients are weighted measures. Degree is the number of ties an individual initiates (outdegree) and receives (indegree), whereas strength weighs the sum value of these initiated (outstrength) and received (instrength) ties (Wasserman and Faust 1994). Both degree and strength are built from directional networks (following Fuong et al. 2015). Closeness centrality measures the inverse of the topological shortest distance between a focal node and all other individuals in the group (Yang et al. 2016). Closeness is additionally broken down into the ability of other individuals to reach the focal individual (incloseness) and the ability of the focal individual to reach all other individuals (outcloseness). Betweenness centrality evaluates the number of shortest paths that pass through a focal individual in undirected networks to determine the significance of an individual’s position in the control of information or disease within their group (Wey et al. 2008). Eigenvector centrality quantifies the broader connectedness of a focal individual by accounting for secondary connections, or the interactions between “friends of friends” (Wasserman and Faust 1994; Yang et al. 2016). Average shortest path length measures the average number of individuals that lie on the shortest path between a focal individual and another individual in their network (Newman 2010). It describes how efficiently individuals connect to other members of their network and less social individuals have larger negative average shortest path lengths (Newman 2010). Lastly, clustering coefficients measure the cliquishness of a network by dividing the actual number of relationships formed by a focal individual by the total number of potential relationships they could form (Wey et al. 2008). The local clustering coefficient analyzes the embeddedness of a single individual within their local network (Wasserman and Faust 1994; Yang et al. 2016). Local clustering coefficients are calculated by taking the number of ties the focal individual had and dividing it by the maximum potential number of ties (Wey et al. 2008; Mady and Blumstein 2017). Global clustering describes the density of the network or how connected an individuals' first degree connections are connected to each other (Barrat et al. 2004). A high degree of global clustering indicates that an individual is embedded in groups that are smaller and more exclusive than the larger network.

For my studies, interaction networks were first filtered for transient individuals (individuals who were observed <5 times per year), pups (who are born halfway through summer and are only present for part of the time period recorded) and unknown individuals. Observations were separately categorized by affiliative behaviors (e.g., play, allogrooming, sitting together) and agonistic behaviors (e.g., fighting). Observations were converted into interaction matrices, from which the above mentioned social network measures were extracted through the igraph package in R (Csárdi and Nepusz 2006).

Although it is common to study the effects of specific social relationships on fitness outcomes, the effects of sociality can vary broadly between species. For instance, strong affiliative relationships help us humans live longer (Umberson and Montez 2011), but they decrease life span in yellow-bellied marmots (*Marmota flaviventer*, Blumstein et al. 2018). Thus, it is important that we examine how specific social relationships shape individual behavior in species with different types of sociality.

Yellow-bellied marmots are a hibernating sciurid who live in harem polygynous colonies (one male, many females and offspring) and during their second summer, all males and about half of the females disperse (Armitage 2014). They occupy a vast expansion of the western United States, living in such diverse habitats as alpine and subalpine meadows and in the high desert. As generalist herbivores, they forage on a wide variety of herbs and forbs along with the occasional car brake line. One the least social of the 15 species of marmots around the world, the sociality and life history of yellow-bellied marmots have be studied since 1962 at the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado, USA (38° 770 N, 106° 590W) (Armitage 2014). As facultatively social mammals, marmots may be found in large groups or completely alone. However, unlike other mammals, marmots suffer from a number of negative effects of strong affiliative relationships. Highly affiliative females have less reproductive success, lower longevity, and lower overwinter survival (Wey and Blumstein 2012; Yang et al. 2016; Blumstein et al. 2018). Females become less social as they age and yearlings, who engage in the majority of affiliative interactions, appear to be the social glue that holds marmot social groups together (Wey and Blumstein 2010). But affiliative sociality can help marmots in certain situations, namely in protection against predators. All marmots benefit from large group sizes where many eyes and ears are better at predator detection and alerting everyone through alarm calls (Montero et al. 2020). Yearling females, in particular, benefit from their affiliative relationships and those with stronger affiliative ties to their group are less likely to disperse (Blumstein et al. 2009) and have higher summer survival (Montero et al. 2020). Although less studied, agonistic relationships also impact marmot fitness and agonistic males have higher reproductive success (Wey and Blumstein 2012).

Researchers continuously observe and trap the population at RMBL during their active season from April to September each year. Marmots are trapped biweekly with Tomahawk live traps baited with molasses covered horse feed. Each individual receives a unique pair of metal ear tags for permanent identification and also a dorsal pelage mark using nontoxic Nyanzol-D dye to aid in identification from afar (Blumstein et al. 2009). A number of other measures are taken including behavior during trapping and handling, weight, left hind foot length, reproductive status, genetic (hair) and fecal samples. The population lives in the Upper East River Valley, separated into up-valley and down-valley, two areas with different elevations (down valley ~2870 m, up valley ~2970 m) and snow melt dates and across 12 colonies ranging in size from 1 to 50 individuals (Van Vuren and Armitage 1991; Armitage 2014). Researchers record behavior during peak hours of activity (0700 – 1100 and 1600 – 1800) each day (weather permitting) with binoculars and 45x spotting scopes, which allow researchers to remain ~200 m from most colonies to avoid interference with behaviors. Ethogram defined in Supplementary Table A.1.1. Predator sightings in the valley are continuously recorded by researchers both during sessions and outside of them.

In this dissertation, I examined the effects of marmot social relationships on a number of well-studied fitness associated behaviors. In my second chapter, I assessed whether an individuals' specific affiliative or agonistic social relationships impacted how they responded to predators and in response to trapping. Because these responses are individually-specific, the broader question is how does social network position influence personality traits. In my third chapter, I looked at whether social relationships had a direct or indirect impacts on whether and how individuals solved a novel problem. Finally, and for my fourth chapter, I looked at individual reliance on asocial and social information during foraging.

The social environment impacts anti-predator personality traits

Much like people, an individuals' social relationships, experiences and position in their social group can shape their individual identity: namely, their personality. Animal personality is defined as consistent individual differences in behavior (Sih et al. 2004) and commonly measured personality traits, such as boldness and aggression, have numerous consequences for reproductive fitness, survival and dominance (Smith and Blumstein 2008; Colléter and Brown 2011; Moiron et al. 2020). Individually measured traits, such as aggression against conspecifics, can have carry over effects across contexts, such as when highly socially aggressive individuals are also aggressive against predators (Van Oers et al. 2005), or time, where an individual may have consistent levels of docility throughout their life (Petelle et al. 2013). These cross-context correlations are considered behavioral syndromes (Sih et al. 2004). Both personality traits and the formation of behavior syndromes may be structured by external or internal factors (Smith and Blumstein 2013), such as three-spined sticklebacks (*Gasterosteus aculeatus*) who only form an aggression behavioral syndrome between social and anti-predator aggression after exposure to predators (Bell and Sih 2007; Herczeg et al. 2009).

Predation is a major ecological factor that shapes individuals' lives by altering their behavior patterns, their social group composition, and creating an environment of fear through the threat of death (Luttbeg and Sih 2010). Individuals consistently vary in their ability to perform anti-predator behaviors (Cressler et al. 2015) and these consistent differences lead to anti-predator personality traits (Horváth et al. 2020). However, individual anti-predator responses are likely largely influenced by their social environment. Protection from predation is a major reason why individuals form social groups (Hamilton 1971; Caro 2005), but living in social groups can lead to altered individual risk-resource trade-offs (Hamilton 2004; Bolnick and Preisser 2005). Social groups create scenarios of competition (Goss-Custard 1980) over forage, mates or territory, which can lead to more risky behavior. For instance, dominant vervet monkeys (*Chlorocebus pygerythrus*) increase their likelihood of encountering new food by foraging along group edges where they are also more likely to encounter predators (Teichroeb et al. 2015). However, even more specific social relationships including fear of aggression or social security can influence these behaviors. Overall, dynamic affiliative and agonistic relationships in the wild likely have specific effects on individual behavior (Snijders et al. 2014; Díaz López 2020) and subsequently affect life history, through external pressures such as predation, influencing the adaptive value of sociality. In my first chapter, I looked at how an individuals' social environment impacted their consistent, repeatable responses to predators.

I measured the consistency of two anti-predator traits previously measured in the yellow-bellied marmot system: "boldness", a measure of risk-taking behavior, and "docility", a measure of defensive aggression (Petelle et al. 2013; Blumstein et al. 2013). This study was conducted on data collected from 2002 to 2019. Boldness was calculated from flight initiation distance, the distance at which an individual will flee from an approaching researcher, who functions as a simulated predator. In this context, bolder individuals have shorter flight initiation distances, allowing "predators" to approach closer. This response is part of an economic risk-foraging trade-off, where individuals must make optimal decisions between obtaining resources (i.e., forage, mates, territory) and their predation risk (Ydenberg and Dill 1986; Lima and Dill 1990). Bolder individuals take greater risks by maximizing their time engaging in a resource related activity with the trade-off of allowing a predator to approach closer and risk a fatal or injurious encounter. Docility was a rank score of how reactive an individual was to trapping and handling (Réale et al. 2000; Petelle et al. 2013). Individuals were dichotomously scored (i.e., 0/1) by whether they struggled in the trap, alarm called, tooth chattered, walked into the handling bag or tried to bite the researcher, all of which are indicative of fear reaction (Smith et al. 2012). These behavioral reactions were summed and then subtracted from the maximum potential count (5) to create the docility score. Individuals scoring high on the docility score (5) were more docile, while those scoring low on the index (0) were less docile. Boldness was moderately repeatable by individual (0.556) and docility had low repeatability (0.252). Both of these personality traits had previously been found to be stable across life stages (yearling and adult) but did not form a behavioral syndrome (Petelle et al. 2013; Blumstein et al. 2013).

I then fitted bivariate generalized linear mixed models to examine how these two anti-predator personality traits correlated with an individuals' position in their social network. In particular, I separately analyzed the individuals' agonistic and affiliative networks to capture the different effects that these types of social relationships can have on an individual. Agonistic relationships, such as bullying by a dominant individual, can incite fear within individuals, altering their behavior or excluding them from resources that may cause subordinates to have different priorities in a risk-resource trade-off (Goss-Custard 1980; Giraldeau and Caraco 2018). Affiliative relationships, on the other hand, often provide a number of benefits, including social security (Blumstein et al. 2017) and lower stress (Brent et al. 2011), which can also alter the ways in which an individual will react to a threat. As we know, marmots typically suffer fitness costs from affiliative relationships, with the exception of the predator detection benefits offered by group size. I wanted to know whether 1) social aggression was tied with either defensive aggression or boldness and 2) whether the anti-predator benefits of affiliation influenced an individuals' anti-predator responses.

After controlling for a number of fixed effects, I found that docile individuals initiated aggression against fewer individuals and were less central in their agonistic networks. However, docility was not influenced by affiliative behaviors and neither aggression nor affiliation influenced boldness. Marmots who do not interact aggressively with others are less (aggressively) reactive towards a predator, but individuals do not alter how close they will allow a predator to approach based on social relationships. The latter suggests that marmots either are not resource-limited by social aggression or are not willing to increase risk by predators to secure extra resources. Additionally, the overall lack of effect of affiliative relationships contributes to evidence that marmots lack a sense of social security conferred by specific affiliative relationships. These results indicate that social environment does influence anti-predator behavior but that its effects are not uniform across all types of anti-predator responses.

Bullied marmots are worse problem-solvers

In addition to predation, foraging is an essential goal of life, especially for hibernators who have a short period of time to put on extra weight to survive long periods of deep torpor. However, animals must learn to locate, identify, manipulate and consume food in a dynamic environment. In particular, individuals may increase their reward by taking risks, such as consuming novel food sources or devising more efficient ways to consume familiar foods. When these food sources come with challenges, individuals can overcome them through innovation, where individuals devise novel solutions or behaviors to deal with problems (Reader and Laland 2003). However, individuals adapt to challenges in different ways governed by their internal or external circumstances and experiences. For instance, neophobic individuals, who have an aversion to novel stimuli, are less likely to interact with a novel object making them worse problem-solvers (Benson-Amram and Holekamp 2012; Benson-Amram et al. 2013). Persistent individuals who spend more time trying to solve a problem (Keagy et al. 2009; Thornton and Samson 2012; Chow et al. 2016), behaviorally diverse individuals who try out more types of behaviors (Griffin et al. 2014; Daniels et al. 2019) and behaviorally selective individuals, who tend to focus on effective behaviors (Chow et al. 2016; Daniels et al. 2019), are all better problem-solvers. But the expression of these behaviors or interaction with a puzzle may be governed by an individuals' social environment.

Specific social relationships matter and they can act in both direct and indirect ways. The necessity drives innovation hypothesis (Reader and Laland 2003) states that dominant or aggressive individuals may directly impact subordinate problem-solving by restricting access to easily accessible food sources, forcing subordinates to problem solve (An et al. 2011). In the social inhibition hypothesis (Overington et al. 2009; Griffin et al. 2013) dominate individuals directly impact problem-solving in subordinates preventing interaction. This environment of fear can also indirectly affect problem-solving by interfering with problem-solving behaviors, such as behavioral diversity or behavioral selectivity. Conversely, affiliative behaviors may increase information transmission (Kulahci et al. 2016), leading to learning, sharing of resources, and scrounging . Thus, I examined whether an individuals' affiliative or agonistic social relationships directly or indirectly affected the behaviors used when problem solving and whether this influenced their eventual success.

To test how an individual behaves when confronted with a novel extractive foraging task, I constructed and deployed eight wood-framed, plexiglass puzzle boxes (30.84 x 30.84 x 30.84

cm, Figure 1). Each box could be solved in two ways: by pushing up on a small plexiglass projection on the lid of the box, or by pulling open a hinged door on one side. Both openings were designed to mimic behaviors already in the marmots' repertoires, but they allowed us to test slightly different applications for each solution (e.g., pulling the door open with mouths or forepaws or pushing the lid up primarily with mouth and nose). Additionally, having two solutions allowed us to examine whether social transmission differed between an easy (lid) and difficult (door) solution. Both solutions were held shut by two 5.08 cm Velcro strips to increase the difficulty and prevent accidental opening. To prevent marmots from flipping the apparatus, each box was secured to a 60.7 x 50.8 cm plywood platform. Both the wooden frame and plywood were sealed with two coats of polyurethane to prevent water damage and to permit cleaning with concentrated acetic acid to remove any smells between deployments to different colonies. Puzzle box shown in Figure 2.1.

Social network measures are often highly correlated and I did not have specific hypotheses for each measure, so I first reduced dimensionality among them using a principal component analysis. This resulted in three affiliative and three agonistic components. For affiliative relationships, individuals were scored on *friendliness* (in/out degree, in/out strength and eigenvector centrality), *isolation* (negative betweenness centrality), and *initiated closeness* (out closeness). For agonistic relationships, individuals were scored on *aggression* (out degree, betweenness centrality, eigenvector centrality and in/out closeness), *received aggression* (in degree, in strength) and *initiated aggression frequency* (out strength). Then, I extracted information on problem-solving from video recorded interactions with the puzzle box in 2018. First, all videos were scored for interaction behaviors that defined which body part or behavior was used to interact with the box and which part of the box was contacted (i.e., individual used their nose to interact with the puzzle box lid, full ethogram outlined in Supplementary Table A.1.1). These behaviors were then used to calculate four common behavior measures associated with cognition and problem-solving: behavioral selectivity, behavioral diversity, persistence and neophobia. Behavioral selectivity was calculated as the proportion of time in sight that an individual spent interacting with the box during a trial, which was a temporally isolated approach to the box. Behavioral diversity was calculated with the Shannon index (Pielou 1975) as the diversity of behaviors used during a trial. Persistence was measured as the proportion of time spent in sight during a trial that an individual spent interacting with the box. Neophobia, typically a measure of fear of a novel object or situation, had to account for potential habituation over trials and so was measured only on the first trial of each day that the individual interacted with the puzzle box. It was measured as the latency from when they first stepped onto the platform to when they first made contact with the box. Overall problem-solving was a binary measure of whether an individual succeeded in obtaining food on their own by either opening the lid or the door during a trial. I then fit both direct (generalized linear mixed models) and indirect (structural equation models) to measure the relationships between an individuals' social network measures, the behaviors they used to interact with the box during a trial and whether or not they ultimately succeeded in solving the puzzle box during that trial. The direct models looked at whether problem-solving succeed correlated with any of the six PCA social measures or the four interaction behaviors. Individuals who receive greater amounts of aggression were worse problem-solvers and those who used a greater diversity of behaviors were more successful problem-solvers. For the indirect models, the six PCA social measures predicted problem-solving success mediated by the four interaction behaviors. Aggression particularly decreased how persistent, behaviorally flexible and the diversity of behaviors an individual used when trying to solve a puzzle. Thus, an individuals' social environment, particularly when they are the targets of social aggression, alters how an individual approaches a novel problem and ultimately whether they successfully demonstrate problem-solving. This is particularly important to note for studies of cognition and problem-solving in the wild, where social interference during experiments could change individual expression of cognitive abilities. Thus, the line between a "smart" and "not smart" individuals may not truly reflect underlying cognitive ability.

Marmots learn where to forage, but not how to forage

Before you can use a number of different strategies to solve a foraging problem, you first need to find it. Macaques wash sweet potatoes (Hirata et al. 2008), chimpanzees use sticks to get at tasty ants (Goodall 1968) and great-tailed grackles (*Quiscalus mexicanus*) eat dead insects from car license plates (Grabrucker and Grabrucker 2010). These novel behaviors or skills can be passed on in different ways. For most animals, for whom insight- the spontaneous reproduction of behaviors- is out of reach, trial and error aided by different forms of learning is the way to develop these skills. Whether it's a particularly ripe mango tree or a nut covered in a spiny exterior, animals use learning to avoid wasting time, energy and increasing their risk of predation while trying to stumble across random solutions to their problems (Sol and Lefebvre 2000; Greggor and Thornton 2016; Reader 2016). Animals can learn on their own (asocial learning or trial and error) or they can learn from others (social learning). These each come with their own set of costs and benefits. Like a grad student using R packages of compiled functions from other researchers, social learning can cut down on all the excess time and energy (and risk for animals- grad students don't have to worry about predators sneaking up on them while coding!) that goes into learning or doing something yourself (Galef and Laland 2005). However, a mistake in an R package made by someone else could lead to incorrect results (and rejected papers!) whereas building the function yourself would allow for more intimate knowledge of the functions and a higher change of catching those kinds of mistakes (Giraldeau et al. 2002). Like struggling grad students, animals must also make these decisions between costly yet accurate asocial information and easy but potentially incorrect social information (Kendal et al. 2005). However, the learning process can occur over multiple steps or through different access points and an individual may use social learning to obtain information in one context but asocial learning in another. This can include forms of learning such as *local enhancement*, where individuals are drawn to an object or area by the presence of others (Galef 2015), *stimulus enhancement*, where an individuals' attention is drawn to an object or area by a conspecifics' behavior or *emulation*, where an individual learns of a goal (e.g., opening a puzzle box) from another individual but does not copy the process they use to get to that goal (e.g., copying a motor pattern, Heyes and Galef Jr. 1996).

For my last chapter, I studied how marmots used information in the context of a novel foraging puzzle. I asked three questions: 1) Do marmots show evidence of learning by becoming more efficient puzzle box solvers over time? 2) Do individuals socially transmit information on the location of the puzzle box? 3) Do individuals socially transmit information on the solutions to the puzzle box? I first examined whether individual marmots became more efficient at solving a problem with experience, indicative of asocial learning, using a series of generalized linear mixed effects models. I used three measures to test for individual learning in our population. The first, 'latency to open the box', was a temporal measure of efficiency where time to open the box should decrease with increasing experience (Thornton and Samson 2012; 'work time' in Benson-Amram and Holekamp 2012; Cauchard et al. 2013; 'problem-solving efficiency' in Chow et al. 2016). To obtain this measure, we subtracted the time that the individual first interacted with the box from the time it took to open the box. The second, ‘selective persistence’, also known as ‘behavioral selectivity’, measures efficiency and is defined as the percentage of effective behaviors (i.e., touching the door or lid) used by an individual out of all behaviors used when interacting with the box ('behavioral selectivity' in Chow et al. 2016; Quigley et al. 2021). Selective persistence is predicted to increase with experience as individuals learn which behaviors are most effective for opening the box. The third, ‘non-selective persistence’, measures the rate of interaction with the box and is defined as the total number of contacts with the box divided by the total time spent with the box during a trial ('persistence' in Chow et al. 2016; Quigley et al. 2021). Non-selective persistence is predicted to decrease with increasing successful trials as individuals use fewer behaviors to solve the problem. I found that individuals do not show a neat downward trend in efficiency with experience, suggesting that individuals do not “learn” to solve the problem by remembering and repeating their behaviors but they do become better over time, suggesting that while they are approaching the problem as a novel obstacle each time, they do remember some of the ways in which they solved it before.

I then used network-based diffusion analysis (NBDA) to test whether and what type of information individuals spread socially. NBDA uses social networks and order of event acquisition to estimate the likelihood that a trait was passed between group members socially or was obtained by each member individually. I specifically used NBDA to test for the social transmission two events: when an individual first encountered the puzzle box and when they first opened the box using the lid or the door solution. The two years of the study, 2018 and 2019, were tested separately and a different transmission rate was estimated for each colony. When it comes to social learning, marmots appear to be typical rodents. When faced with obtaining information on where a novel food source is (location) and how to obtain that food source (technical skill), they more frequently learn the location while only rarely learning the technical skills associated with access.

Conclusions

Together these studies have shown that aggressive but not affiliative relationships are associated with important fitness-related behaviors in yellow-bellied marmots. Specific types of aggressive relationships are associated with how much risk they are willing to take, how well they problem-solve and which behaviors they use to do so. However, the social network approach I took to examine the role of social relationships identified no single network trait that was important: outdegree and eigenvector centrality explained variation in docility while instrength and a principal component composed of outdegree, betweenness, outcloseness, incloseness and eigenvector centrality explained variation in problem-solving. Local clustering, a trait that describes the broader network structure explained no significant variation which suggests the relative importance of individual versus network social measures on behavior could be the focus of future studies. While I found some variation was explained by agonistic relationships, I found that no variation was explained by the nature of affiliative relationships. This is notable because social relationships have been shown to explain a variety of behavioral traits in other species (Kulahci et al. 2016;). The trend towards using social transmission of location of food sources suggests that unlike other species where affiliative relationships based on reciprocal grooming are associated with information sharing, marmots may just eavesdrop on others; a behavior that might be better explained by tolerance for others. Ultimately, I have shown that the nature of an individual's social relationships is associated with how individuals react to predators, their problem-solving strategies and whether they engage in socially transmission of information. Together this illustrates the utility of using formal social network analyses. Relationships matter.

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Chapter 2: Docility but not boldness associated with social aggression in yellow-bellied marmots

Abstract

Individuals respond to predators through an array of anti-predator behaviors that can be influenced by their social environment, specifically through protection from predators or by altering risk-resource trade-offs through competitive exclusion from resources. While social effects like group size are well studied, the specific ways in which different types of relationships, such as number of interaction partners or centrality in their group, influence consistent anti-predator behaviors is less understood. However, the effects of social relationships on behavior are not uniform between species or even between individuals. Here, we examined how an individual's affiliative and agonistic social relationships impacted two personality traits related to anti-predator behavior (boldness and docility) in yellow-bellied marmots (*Marmota flaviventer*), a facultatively social species with unusual negative impacts of affiliative relationships. We found that docile individuals were less involved in aggressive interactions either by avoiding or being excluded from aggressive interactions. Boldness was not associated with aggression, suggesting that individuals are either not resource limited by social aggression or are not willing to risk more predator exposure to secure those resources. Affiliative relationships were not associated with docility or boldness, contributes to other findings that marmots have a limited sense of social security from affiliative relationships.

Introduction

Animal personalities are defined as consistent among-individual differences in behavior (Sih and Bell 2008) and personality traits, such as boldness, aggression, exploration, and sociability, may impact individual fitness (reproductive success: Smith and Blumstein 2008, survival: Moiron et al. 2020, invasion potential: Chapple et al. 2012, survival: Moiron et al. 2020, dominance: Colléter and Brown 2011). Furthermore, there may be carryover effects of behaviors between situations, such as when individuals with high social aggression also engage in high levels of aggression against predators, creating a behavioral syndrome (Sih et al. 2004; Van Oers et al. 2005). Both personality and behavior syndromes can be shaped by multiple factors, including external stimuli or internal experience (Wolf and Weissing 2012; Smith and Blumstein 2013). For instance, three-spined stickleback (*Gasterosteus aculeatus*) only develop an aggression syndrome between social and defensive (anti-predator) aggression after individuals are exposed to predation pressure (Bell and Sih 2007; Herczeg et al. 2009). Other factors such as familiarity and size of conspecifics (Conrad et al. 2011) or group size (Piyapong et al. 2010) can also alter the adaptive value and structure of a behavioral syndrome. Indeed, behavioral syndromes are likely influenced by multiple factors.

Predation is a major ecological factor that influences individual behavior and survival (Luttbeg and Sih 2010), but individuals vary in their ability to perform costly anti-predator behaviors like predator escape (Cressler et al. 2015). In some cases, this may be due to variation in intrinsic ability. Carpetan rock lizards (*Iberolacerta cyreni*) compensate for shorter legs by being more likely to fight in response to a predator (Horváth et al. 2020). Similarly, slow running yellow-bellied marmots (*Marmota flaviventer*) make a trade-off by prioritizing foraging over vigilance to decrease time spent exposed (Blumstein et al. 2010). Individual variation in anti-predator behavior is typically repeatable (Carrete and Tella 2010; Davidson et al. 2018) and can correlate with other personality traits, such as activity levels (Jones and Godin 2010). However, anti-predator behavior is not often studied as a personality trait itself (Horváth et al. 2020). Two common, repeatable measures of anti-predator behavior are flight initiation distance, a measure of risk-taking, and defensive aggression, a response to trapping and handling. Flight initiation distance is the distance at which an individual will flee from the approach of a simulated predator (Ydenberg and Dill 1986; Lima and Dill 1990). Defensive aggression occurs when behaviors seen in social contexts or other fear-based aggression contexts are redirected towards predators or threats (Blumstein et al. 2013b).

Aside from intrinsic variation, an individuals' social environment can also shape anti-predator behavior by providing protection from predation (Hamilton 1971; Caro 2005) or by altering risk-resource trade-offs (Hamilton 2004; Bolnick and Preisser 2005). Individuals living in groups may take more risks because of competition around food sources (Goss-Custard 1980) or because there is lower individual predation risk in a group (dilution hypothesis – (Pulliam 1973; Elgar 1989). Specific relationships that individuals form within their groups lead to unequal distribution of social benefits and costs of group-living contributing to individual variation in anti-predator behavior. For instance, dominant vervet monkeys (*Chlorocebus pygerythrus*) forage along the edges of groups where they were more likely to obtain food but also more likely to encounter predators (Teichroeb et al. 2015). Giraffes (*Giraffa camelopardalis*) altered scanning behavior with social group composition, increasing vigilance when larger bulls were present (Cameron and Du Toit 2005). Relationship strength is associated with predator inspection, latency to return to foraging after alarm calls, and reactivity to a threat (Croft et al. 2006; Blumstein et al. 2017; Nadler et al. 2021). An individuals' social network provides precise measures of an animal's social relationships in their natural environment. Social network measures quantify relationships beyond simple dyadic interactions, allowing researchers to assess the influence of specific components of relationships such as amount of contact between two individuals or how central an individual is to their network (Croft et al. 2008; Wey et al. 2008; Pinter-Wollman et al. 2014). Different types of social interactions, such as affiliative and aggressive relationships, also have different effects on behaviors (Snijders et al. 2014; Díaz López 2020). For instance, aggressive relationships may increase risk-taking behavior because individuals are otherwise excluded from resources (Goss-Custard 1980; Giraldeau and Caraco 2018) while stronger affiliative relationships increase health outcomes(Umberson and Montez 2011) or sense of social security (Mady and Blumstein 2017). It is important to study how these relationships interact with external pressures such as predation and food competition because individual differences in behavior shaped by social relationships likely influence the adaptive value of sociality.

Yellow-bellied marmots (hereafter, marmots) are a ground-dwelling sciurid rodent that have been well-studied in the wild (Armitage 2014). Marmots are facultatively social and, contrary to most social mammals, experience largely negative effects of strong affiliative relationships including decreased reproductive success, longevity, and survival (Wey and Blumstein 2012; Yang et al. 2016; Blumstein et al. 2018), but benefit from overall sociality through predator detection and alarm calling (Montero et al. 2020). Social groups are structured around kin relationships with yearlings engaging in the majority of affiliative behaviors that hold groups together, while older female marmots become more agonistic as they age (Wey and Blumstein 2010). This complex relationship with affiliative and agonistic sociality make them an ideal species in which to study the interaction between individualistic anti-predator behavior and social network position. Marmots are known to exhibit consistent individual differences in both boldness, measured as flight initiation distance, and docility, measured as the inverse of defensive aggression (Blumstein et al. 2013b), across life stages as yearlings and adults, but the two personality traits together do not form a behavioral syndrome (Petelle et al. 2013). Previously, defensive aggression was not found to correlate with several measures of agonistic sociality, including measures of tendency to initiate or receive aggression, suggesting that defensive and social aggression can evolve separately (Blumstein et al. 2013b). Additionally, there is no relationship between glucocorticoid levels and social attributes, suggesting that marmots do not become physiologically stressed over agonistic social interactions (Wey and Blumstein 2012; Blumstein et al. 2018), which may interfere with extrapolation of the behavior to other stress-inducing contexts such as predation. Lastly, defensive aggression was not state-dependent but did have positive feedbacks from mass and age (Petelle et al. 2019).

Here we use bivariate models to expand on previous work on marmot personality to determine whether there is an association between specific social network measures in affiliative and agonistic contexts, and two individually repeatable measures of anti-predator behavior: boldness (calculated from flight initiation distance) and docility (response to trapping and handling). Overall, we hypothesize that affiliative relationships will represent an individuals' sense of social security while agonistic relationships relate to the effects of a competitive environment in a social risk-reward tradeoff. By separately analyzing affiliative and agonistic network measures, we can potentially infer how these different social relationships are associated with individual-specific anti-predator traits.

Methods

Study Site and Species

We studied yellow-bellied marmots in and around the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado, U.S.A. (38° 770 N, 106° 590W). Marmots have been studied in this location since 1962 (Armitage 2014); however we focused our analysis on data collected between 2003 and 2019; an interval during which we focused intensively on collecting social interaction data Yellow-bellied marmots live in matrilineal, facultative social groups, and usually occupy subalpine slopes and meadows (Frase and Hoffmann 1980; Armitage 2014). Colonies can be composed of multiple social groups that vary in composition and size. Our primary study site was the Upper East River Valley, which is divided into up- and down-valley sites that differ in the length of their winter and hence the duration of their summer growing season (Van Vuren and Armitage 1991). Overall, we observed 12 separate colonies which were defined by physical separation and a lack of overlapping social interactions.

We aimed to trap marmots biweekly with Tomahawk live traps. Once trapped, they were permanently marked with unique individual ear tags and we applied fur marks to their dorsal pelage using nontoxic Nyanzol-D dye to aid in identification from afar (Blumstein et al. 2009). Weather permitting, we conducted behavior sampling where we quantified social observations on marmot colonies 2-6 h each day during peak activity (0800 – 1100) with binoculars and 15-45× spotting scopes.

Quantifying traits and other correlates

Boldness: Following a previous study on personality in yellow-bellied marmots (Petelle et al. 2013), we defined boldness as the inverse of the flight initiation distance (FID): bold animals tolerated closer approach than shy animals. Flight initiation distance is the distance at which an animal begins to flee an approaching threat (Ydenberg and Dill 1986; Cooper Jr and Blumstein 2015) and is a measure of risk-taking, whereby individuals with larger flight initiation distances prioritize safety over rewards, such as foraging or potential mating opportunities. Between 2003 and 2019, we recorded marmot flight initiation distance during simulated predator approaches. Flight initiation distances were measured at most once per day per individual. The researcher would arrive at a colony and wait quietly for a minimum of five minutes to ensure the animals were exhibiting normal behavior and to avoid habituation to approach stimuli. After identifying the target individual, the researcher walked at a measured pace of 0.5 m/s towards the subject. The researcher dropped a flag to mark their starting distance, the target individuals' alert distance and their flight initiation distance. Alert distance was the distance at which the target individual became vigilant, noted as obvious turning of body or head towards researcher, and was later used to account for variation in flight initiation distance; flight initiation distance was the distance between the researcher and the animal when the marmot fled (Frid and Dill 2002). An individuals' flight initiation distance was measured 1-9 times per year. Distance to burrow, the distance between the subject's initial location and the escape burrow, was also recorded to account for risk. The repeatability of boldness (FID) was determined using the rptR package (Stoffel et al. 2017).

Docility: Following previous definitions of docility (Réale et al. 2000; Petelle et al. 2013, 2019), we calculated docility as a sum of the occurrence of a suite of behavioral responses to trapping. An individual's docility was composed of five behaviors dichotomously scored (i.e., 0/1) while trapping: alarm calling, tooth chattering, struggling in the trap, biting the cage, and attempt to escape by immediately entering the handling bag (Petelle et al. 2013, 2019). Docility may be a measure of defensive aggression (Reale et al. 2007). Glucocorticoid studies show that struggling in the trap is associated with fear (Smith et al. 2012). Once summed, the individual's total score was subtracted from the maximum potential count (5) to create their docility index score. Thus, the most docile individuals would score 5, whereas the least docile individuals would score 0. Individuals were trapped 1-25 times per year. The repeatability of docility was determined using the rptR package (Stoffel et al. 2017).

Predator Pressure: The presence of predators may influence whether individuals are bold in a given year and at a given colony site (Brown et al. 2013; Petelle et al. 2013; Mady and Blumstein 2017). All predators noticed by observers were recorded at each colony. We first separated observations for each year and quantified predation pressure using a colony's 'predator index' by dividing the proportion of observation sessions when a predator was detected at a colony site by the total number of observation sessions in a given year. We then used a median split to differentiate relatively high predator pressure colonies from relatively low predator pressure colonies. The primary marmot predators (Armitage 2014) found at our sites were black bears, *Ursula americanus*, mountain lions, (*Puma concolor*), coyotes (*Canis latrans*), red foxes, (*Vulpes vulpes*), red-tailed hawks (*Buteo jamaicensis*) and golden eagles (*Aquila chrysaetos*).

Dominance: We used the Clutton-Brock index (CBI) to quantify social dominance hierarchies within each year and colony (Clutton-brock et al. 1979). Unlike other metrics of dominance like David's score (DS) and the frequency-based dominance index (FDI), the CBI does not utilize the rate of interaction in its calculation (Bang et al. 2010). As such, the CBI is more applicable to the study of yellow-bellied marmots because it is suited to a species with fewer recorded social interactions (following Blumstein et al. 2013a). The index uses the number of wins and loses an individual has to calculate dominance and is represented as $CBI = (B + b + 1)/(L + l + 1)$. Here, B is the number of individuals one has 'beaten', b is the number of individuals those 'beaten' have won against, L is the number of individual 'winners' with which one has been 'beaten', and l is the number of individuals those 'winners' have 'beaten'.

After calculating the CBI, we computed each individuals' relative rank, which accounts for the number of individuals within the hierarchy (Huang et al. 2011; Blumstein et al. 2013a). The relative rank was found by ordering the CBI values from lowest to highest, giving an absolute rank score for where an individual was positioned in this CBI scale, and then dividing absolute rank by the total number of individuals in the network. For each dominance hierarchy, the lowest relative rank was zero and the highest relative rank was one.

Social Network Traits: We quantified social observations using all occurrence behavior sampling in each colony between mid-April and September. Observations were used to create interaction matrices between all individuals within a colony, which were then used to calculate social network measures. To create interaction matrices, we first filtered data for transient individuals (excluded individuals observed < 5 times during a year), pups (who emerge half way through the active season) and unknown individuals. The resulting dataset consisted of interactions with known initiators and receivers, from which we calculated interaction matrices with directional ties to indicate both connectivity and orientation. Interaction matrices were calculated separately for affiliative behaviors (e.g., play, allogrooming, sitting together) and agonistic behaviors (e.g., fighting, full ethogram in Supplementary Table A.1.1).

From these interaction matrices, we calculated the following social network measures: degree (in and out), strength (in and out), closeness (in and out), betweenness centrality, eigenvector centrality, and local clustering coefficient. Degree, strength, eigenvector centrality, negative average shortest path, and the clustering coefficients were weighted. Degree is the number of ties an individual initiates (outdegree) and receives (indegree), whereas strength weighs the sum value of these initiated (outstrength) and received (instrength) ties (Wasserman and Faust 1994). Both in/out degree and in/out strength were built from directional networks (following Fuong et al. 2015). Closeness centrality measures the inverse of the topological shortest distance between a focal node and all other individuals in the group (Yang et al. 2016). Closeness is broken down into the ability of other individuals to reach the focal individual (incloseness) and the ability of the focal individual to reach all other individuals (outcloseness). Betweenness centrality evaluated the number of shortest paths that pass through a focal individual in undirected networks to determine the significance of an individual's position in the control of information or disease transmission within their group (Wey et al. 2008). Eigenvector centrality quantified the broader connectedness of a focal individual by accounting for secondary connections, or the interactions had by an individual's connections (Wasserman and Faust 1994; Yang et al. 2016). Lastly, the local clustering coefficient analyzed the embeddedness of a single individual within their local network (Yang et al. 2016). We calculated local clustering coefficients by taking the number of ties the focal individual had and dividing it by the maximum potential number of ties (Wey et al. 2008; Mady and Blumstein 2017). Descriptions of all network traits in Table 1.1. All social network attribute analyses were performed in R 3.5.3 (R Core Team 2020) with the igraph package 1.2.4 (Csárdi and Nepusz 2006).

Statistical Analysis

To test the relationship between boldness and docility and social network measures, we fitted a series of bivariate models of boldness or docility with relative rank and 10 different social network measures. We created four datasets, each with a unique combination of docility or boldness and affiliative or agonistic social network traits (i.e., agonistic social network traits and docility form one of the four datasets). Each bivariate model fitted one social network trait and a personality trait as dependent variables. All bivariate models included the random effects of marmot identity and year to account for individual and annual variation. For both social network trait and personality trait, age category (yearling, adult), sex, predator index, relative dominance rank and colony were included as fixed effects to account for individual and environmental effects on sociality and personality. To account for potential habituation effects on docility, days between trapping events at a colony, the number of trapping events at a colony during a year, and the time of day of trapping event (am/pm) were additionally included as fixed effects. To account for potential habituation effects on boldness, days between FID measurements at a colony, number of FIDs within a year at each colony, and time of day FID was collected (am/pm) were also included as fixed effects. Additionally, we included alert distance and distance to burrow as fixed effects only on boldness to account for expected variation in FIDs. All continuous variables were centered and scaled with a mean of zero and a variance of one to permit comparison across traits.

Models were fitted with a Bayesian approach using the MCMCglmm package (Hadfield 2010) in R. We used priors at the correlation level for individual identity effect (i.e., parameter expanded prior: V = diag(2) * 0.02, μ=3, $\alpha.\mu$= rep(0,2), $\alpha.V$ = diag(2)*1000). The priors for year random effects were weakly-informative (V = 1 and μ = 0.002), and the prior for the residual variance was weakly-informative for social traits (V = diag(2), nμ = 1.002). Each bivariate model was run for 1,000,000 iterations (‘nitt’), excluding the first 500 iterations (‘burnin’) and cataloging one in every 100 runs (‘thin’). We examined the variance component plots, levels or autocorrelation (<0.05 per run), and effective sample size (>9995 per run) to ensure we had adequate mixing in our results (Hadfield 2010; Wilson et al. 2010; de Villemereuil 2012; Houslay and Wilson 2017).

Results

Boldness was highly repeatable (0.556±0.034 SE) while docility was somewhat less repeatable (0.252±0.015, repeatability thresholds reviewed in Bell et al. 2009). The agonistic-boldness dataset consisted of 566 observations of 166 individuals. The agonistic-docility dataset consisted of 3,229 observations of 342 individuals. The affiliative-boldness dataset consisted of 562 observations on 165 individuals. The affiliative-docility dataset consisted of 3,170 observations of 340 individuals. After controlling for known relevant fixed and random effects of anti-predator behavior and social measures, we found that there was no association between boldness and an individuals' position in either their affiliative (all credible intervals included 0; Table 1.2, Figure 1.1) or agonistic network (Table 1.3, Figure 1.2). Docility similarly had no association with affiliative network position (Table 1.4, Figure 1.3), but individuals who initiated aggression against fewer others and who were less central in their network were more docile (Table 1.5, Figure 1.4).

For fixed effects, we first focus on fixed effects fitted on social network measures and then on those fitted on boldness and docility. Significance was determined by credible intervals that did not include 0. There was large overlap in results for fixed effects fitted on social network measures across all models. They are presented together here.

Full results for boldness models are in Table 1.6 (affiliative) and Table 1.8 (agonistic) and for docility in Table 1.10 (affiliative) and Table 1.12 (agonistic). Age category was mostly positive when fitted on affiliative social network measures in both boldness and docility models, although only significantly so in some of these models (boldness: outdegree, betweenness, outcloseness, instrength, outstrength and eigenvector centrality, docility: outdegree, outcloseness, instrength, outstrength, local clustering and eigenvector centrality). In the docility model, age category was also negatively and significantly correlated with betweenness. Overall, adults initiated affiliative interactions with more, closer individuals, had more frequent affiliative interactions and moved between affiliative cliques in bold models and received more frequent affiliative interactions from more individuals, received affiliative interactions from close individuals and initiated more frequent affiliative interactions in docile models. Similar to results found in (Wey and Blumstein 2010) where yearlings were central to affiliative networks, in docile models, yearlings were more likely to move between affiliative cliques. For agonistic networks, age category was mostly negative in both boldness and docility models, with the exception of local clustering, which was positive in both. In boldness models, all measures were significant except incloseness and eigenvector centrality, while in docility models all measures were significant. Overall, yearlings were more agonistic both initiating and receiving aggression from more, closer individuals, more frequently, moving between aggressive cliques and living in groups with more aggressive cliques in bold models. In docility models, yearlings were more frequently aggressive with more, closer individuals, moved between aggressive cliques and were more central to their aggressive network. Additionally, adults lived in more aggressive cliques.

Sex was positive in both bold and docile models and significant only in a few (bold: eigenvector centrality model, docile: outdegree and outstrength models). Females were more central to their affiliative networks in boldness models and received more frequent affiliative interaction from more individuals in docility models. Sex was also positive in both boldness and docility models and significant in both agonistic outdegree models and additionally significant in the boldness-outstrength model. Females initiated more frequent agonistic interactions with more individuals, a result previously shown in (Wey and Blumstein 2010), in bold models and received aggression from more individuals in docility models.

Interestingly, there were opposite results in boldness and docility models for yearly predation index. In the boldness-affiliative model, yearly predator index was a negative and significant in the affiliative betweenness and eigenvector centrality models, but was positive and significantly correlated with affiliative indegree, outcloseness and outstrength models in the docility models. In the boldness models, individuals were more likely to move between affiliative cliques and were more central to their affiliative networks during low predator years. In the docility models, individuals initiated affiliative interactions with more individuals and received more frequent affiliative interactions from closer individuals in high predation years. This opposite trend held for the agonistic network models. In boldness-agonistic models, yearly predator index was positive and significant in agonistic indegree, betweenness, instrength models but negative and significant in the agonistic outdegree and eigenvector centrality models. In the docility-agonistic models, yearly predator index was negatively correlated with agonistic outdegree and outcloseness and positively correlated with agonistic instrength and outstrength. For the boldness models, in high predation years, individuals received more agonistic interactions from more individuals and moved between agonistic cliques. In low predation years, individuals initiated agonistic interactions against more individuals and were more central to their agonistic network. But for the docility models, in low predator years, individuals received aggression from more individuals and had aggressive interactions with close individuals and, in high predator years, individuals had more frequent aggressive interactions.

Relative rank similarly had opposite results between boldness and docility models. In the boldness-affiliative models, relative rank was negative and significant only in the affiliative betweenness model, but in the docility-affiliative models, relative rank was positively and significantly correlated in the affiliative indegree, outdegree, betweenness, instrength, outstrength and eigenvector centrality models. However, in the docility models, relative rank was also negatively and significantly correlated in the affiliative incloseness and outcloseness models. This suggests that in the boldness models, subordinate individuals moved between affiliative cliques but in the docility models, dominant individuals both received and initiated more frequent affiliative interactions from more individuals and moved between affiliative cliques and were more central to their affiliative networks, while subordinate individuals both had affiliative interactions with individuals close to them. For agonistic networks, this trend was not continued. In both boldness and docility models, relative rank was positive and significant in several models (boldness: indegree and instrength, docility: indegree, incloseness, instrength and eigenvector centrality). but negative and significant in others (boldness: outdegree and eigenvector centrality, docility: outdegree, betweenness and outcloseness). These results clearly show that dominant individuals received more frequent agonistic interactions from more individuals, while subordinate individuals initiated agonistic interactions against more individuals and were more central to their agonistic network.

For fixed effects fitted on boldness (affiliative: Table 1.7, agonistic: Table 1.9), only alert distance had a negative, significant association with boldness in both affiliative and agonistic models, suggesting that bold individuals allowed closer approach before alerting. In the agonistic model, yearly predator index was also positive in the instrength model, indicating that individuals were bolder in high predator years.

For the fixed effects fitted on docility (affiliative: Table 1.11, agonistic: Table 1.13), age category was negatively correlated with docility in most affiliative and agonistic models but was only significant in a few models (affiliative betweenness and outstrength, agonistic indegree and instrength). This suggests that yearlings were more docile. Relative rank was positively and significantly correlated with docility in all models, indicating that dominant individuals were more docile. Docility was positively correlated with days since last event in all models and negatively correlated with events per year per colony in all models, suggesting that more docile individuals experienced fewer trapping events and more time between events. Time of day (AM/PM) and sex were not correlated with docility. In the affiliative models, yearly predator index was positively and significantly correlated with docility only in the affiliative models in the incloseness and eigenvector centrality models. In high predator years, individuals were more docile. In the agonistic models, yearly predator index was not correlated with docility.

Discussion

We found that more docile individuals were less aggressive, specifically those who initiated aggression against fewer individuals and were less central in their agonistic network. This suggests that docility is correlated with a lack of social aggression where docile individuals either shun aggressive interactions or are shunned by others. Interestingly, a previous study in yellow-bellied marmots found no significant correlation between social aggression and defensive aggression (the inverse of docility; Blumstein et al. 2013b). This may be because we tested this with an expanded set of social interactions on a larger dataset; relatively large datasets may be required to identify relatively small effects. However, our results are not entirely unusual. In other rodents, it has been found that socially non-aggressive individuals typically adopted passive response types such as withdrawal or immobility (Benus et al. 1991) which are akin to docility.

On the other hand, boldness and other measures of risk-taking are expected to correlate with social aggression due to the risk-reward trade-offs of group living whereby competition around food sources increases risk-taking by the losers (Goss-Custard 1980; Giraldeau and Caraco 2018). Support for this hypothesis has been found in a number of species where competition and dominance lead to increased risk-taking (Hegner 1985; Giraldeau and Caraco 2018) to avoid social limitations. However, here we found that boldness, a measure of risk-taking, was unrelated to either the individuals' affiliative or agonistic interactions. This suggests that individual marmots do not suffer serious consequences of socially aggressive behaviors, such as food limitation or physical exclusion, that lead other animals to engage in more risky behaviors. In fact, this may be due to their lack of a defensible foraging resources from which to be excluded as marmots typically eat widely available grass and forbs (Armitage 2014). Previous findings suggest that yellow-bellied marmots do not experience added stress from agonistic interactions (Blumstein et al. 2016). This lack of stress likely means that marmots do not necessarily generalize between socially agonistic interactions and stressful predation situations.

We also provide more evidence that affiliative relationships are not universally beneficial. The formation of social groups is a key anti-predator response (Hamilton 1971; Caro 2005) and social security provided by affiliative relationships with conspecifics can influence risk-taking behavior. Trinidadian guppies (*Poecilia reticulata*) under high predation risk form more stable social relationships (Heathcote et al. 2017), yellow-bellied marmots return to foraging faster after hearing an alarm call from a friendly conspecific (Blumstein et al. 2017), and chimpanzees (*Pan troglodytes schweinfurthii*) alter vigilance depending on whether they have strong affiliative ties with those around them (Kutsukake 2006). However, here we find that neither docility nor boldness were affected by an individuals' affiliative interactions. This result adds to a number of studies identifying the negative or neutral effect of affiliative interactions on yellow-bellied marmots. Previous studies in this species found that social group size increased adult female survival against predators, but not what types of affiliative relationships they had (Montero et al. 2020), and that group size but not social relationships affected variation in vigilance (Mady and Blumstein 2017). Thus, there is no generalization or lasting effect of affiliative social behavior on risk-associated anti-predator behavior in this species.

More broadly, the selection for benefits of strong affiliative social relationships providing social security may be embedded in the type of predator response, being particularly important for species that engage in social mobbing. Also, due to cognitive constraints in individual recognition, there may be a trade-off between larger social groups and more differentiated social relationships (Heathcote et al. 2017). In this case, marmots may prioritize group size over investing energy into collective social defense, of which they only engage in alarm calling. Facultatively social species, such as yellow-bellied marmots, are phenotypically plastic with regards to social interaction and may modify their social structure and relationships according to their environmental conditions (Ulijaszek et al. 1998). Thus, future studies must continue to examine how specific social relationships influence fitness-related behaviors in species across a range of sociality types.

In addition to our general results, we found a number of effects of fixed effects. Yearling marmots were more docile than adults, an unsurprising result, given that yearlings have previously been found to be less aggressive than adults (Wey and Blumstein 2010). This does, however, contradict a previous finding that docility was consistent across age classes (Petelle et al. 2013). However, personality is not always consistent across life stages (Cabrera et al. 2021), and there may be different selection pressures or fitness consequences at different life stages (Groothuis and Trillmich 2011). Interestingly, we also found that dominant individuals were also more docile. This is interesting given that dominant individuals are typically more bold, explorative, aggressive and active (Dingemanse and de Goede 2004; Dahlbom et al. 2011; Colléter and Brown 2011; Rudin et al. 2017). As expected from previous studies, individuals were more docile with fewer, less frequent trapping events (Petelle et al. 2013). Bolder individuals had shorter alert distances which is an important known correlate (Cárdenas et al. 2005).

Our results for fixed effects fitted on social networks showed that adults were more involved in their affiliative networks and yearlings were more involved in their agonistic networks. This is contrary to the results found in (Wey and Blumstein 2010), where marmots were found to become more agonistic as they aged and yearlings were central to affiliative networks. Females were both more involved in both affiliative and agonistic relationships, which makes sense given the polygynous structure of marmot social groups where most individuals are female. Males also may be less involved in social interactions overall. Interestingly, there were opposite results in boldness and docility models for yearly predator index. In boldness models, individuals more affiliative in low predation years, but in docility models, individuals were more affiliative in high predation years. For agonistic relationships, in the boldness models, individuals received more aggression in high predation years and initiated more aggressive interactions during low predation years. In the docility models, individuals received more aggression in low predation years and have more frequent aggressive interactions during high predation years. Lastly, subordinate individuals moved between affiliative cliques in boldness models but dominants were more involved in affiliative relationships in docility models. For agonistic relationships, dominants received more agonistic interactions while subordinates initiated more agonistic interactions.

Our results demonstrate that the social environment provides important context for fitness enhancing activities. For this facultatively social species, we found that aggression, but not affiliative social relationships influence anti-predator behaviors. Thus, the protective aspects of sociality against predation differ between individuals, species and sociality types. Further tests should identify how social context affects anti-predator behavior in species with different types of sociality.

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Figures

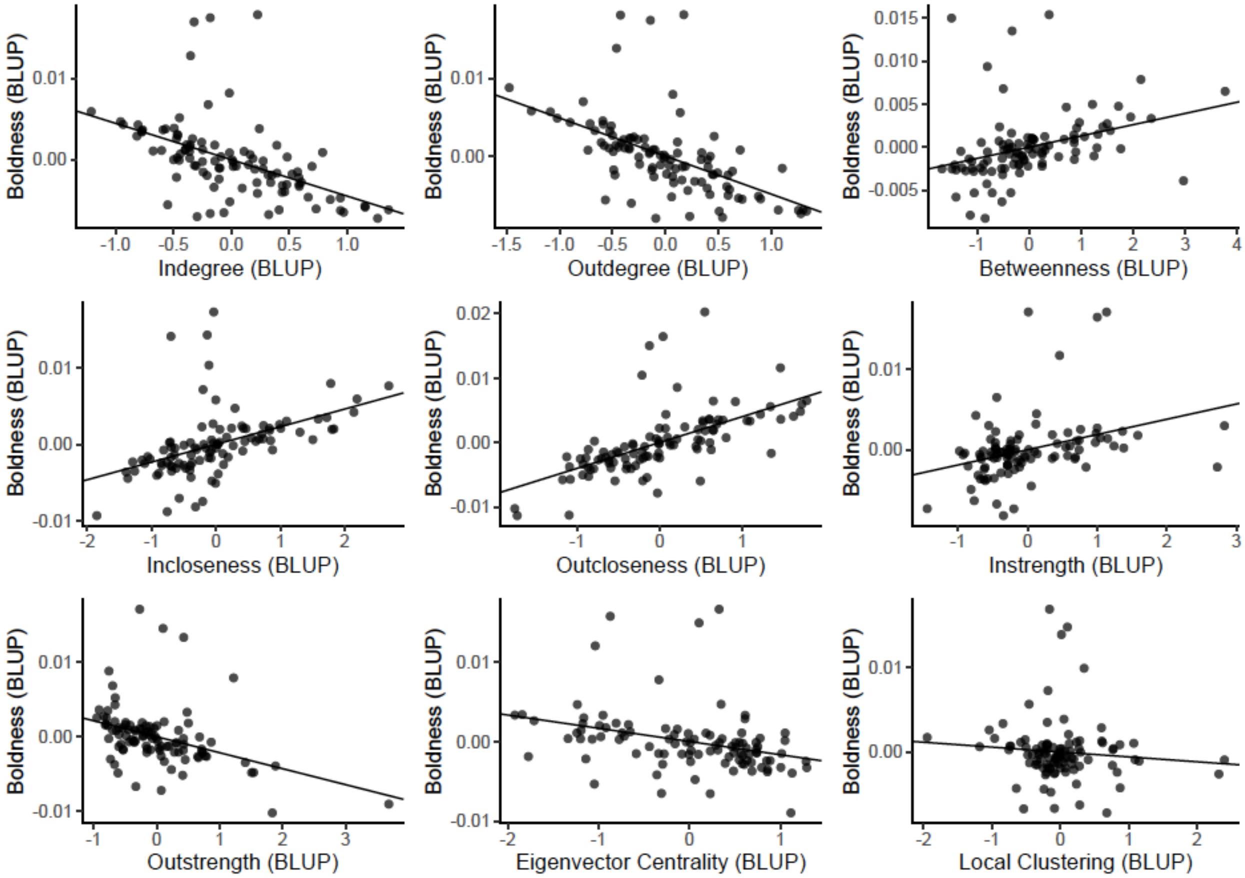

Figure 1.1. Linear regression between best linear unbiased predictions (BLUPs) of affiliative social network traits for each individual and boldness. Bold red lines are significantly different from zero according to Table 1.2.

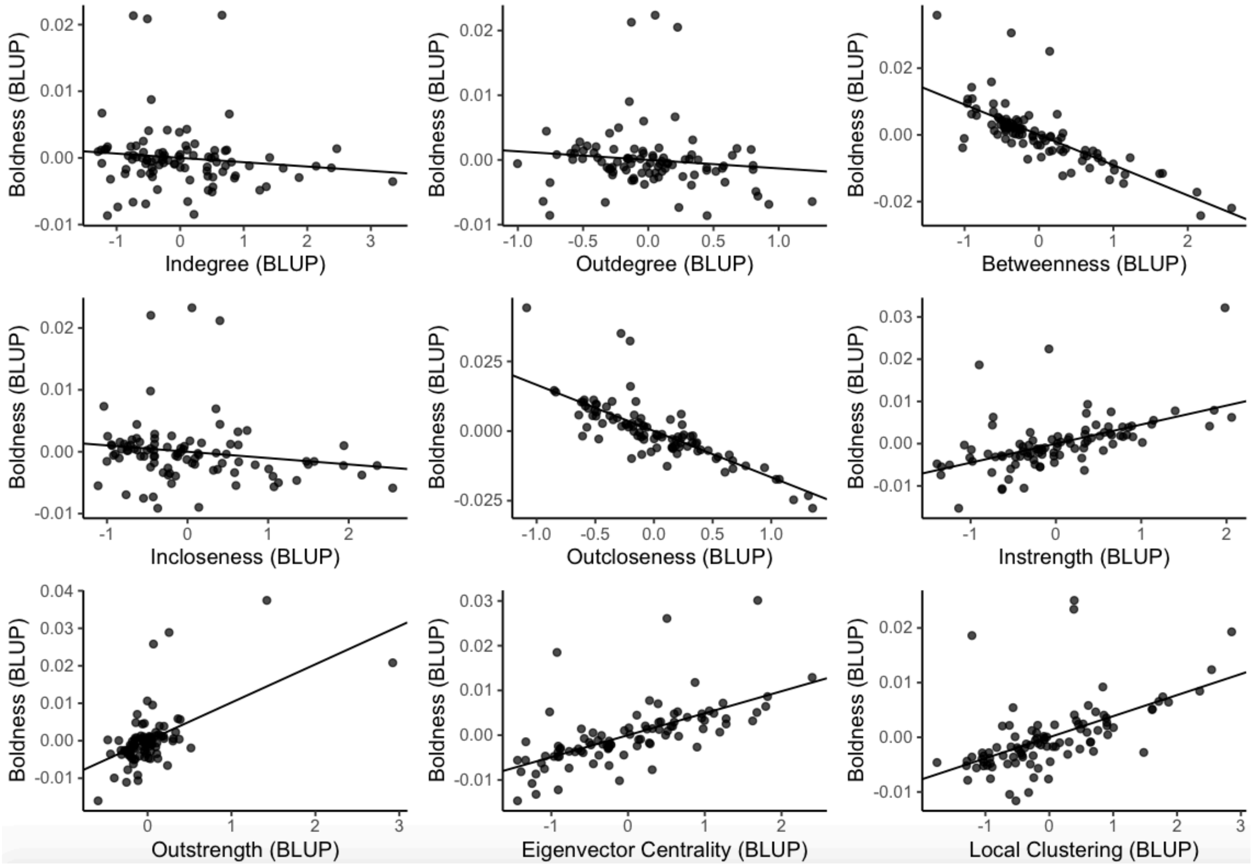

Figure 1.2. Linear regression between best linear unbiased predictions (BLUPs) of agonistic social network traits for each individual and boldness. Bold red lines are significantly different from zero according to Table 1.3.

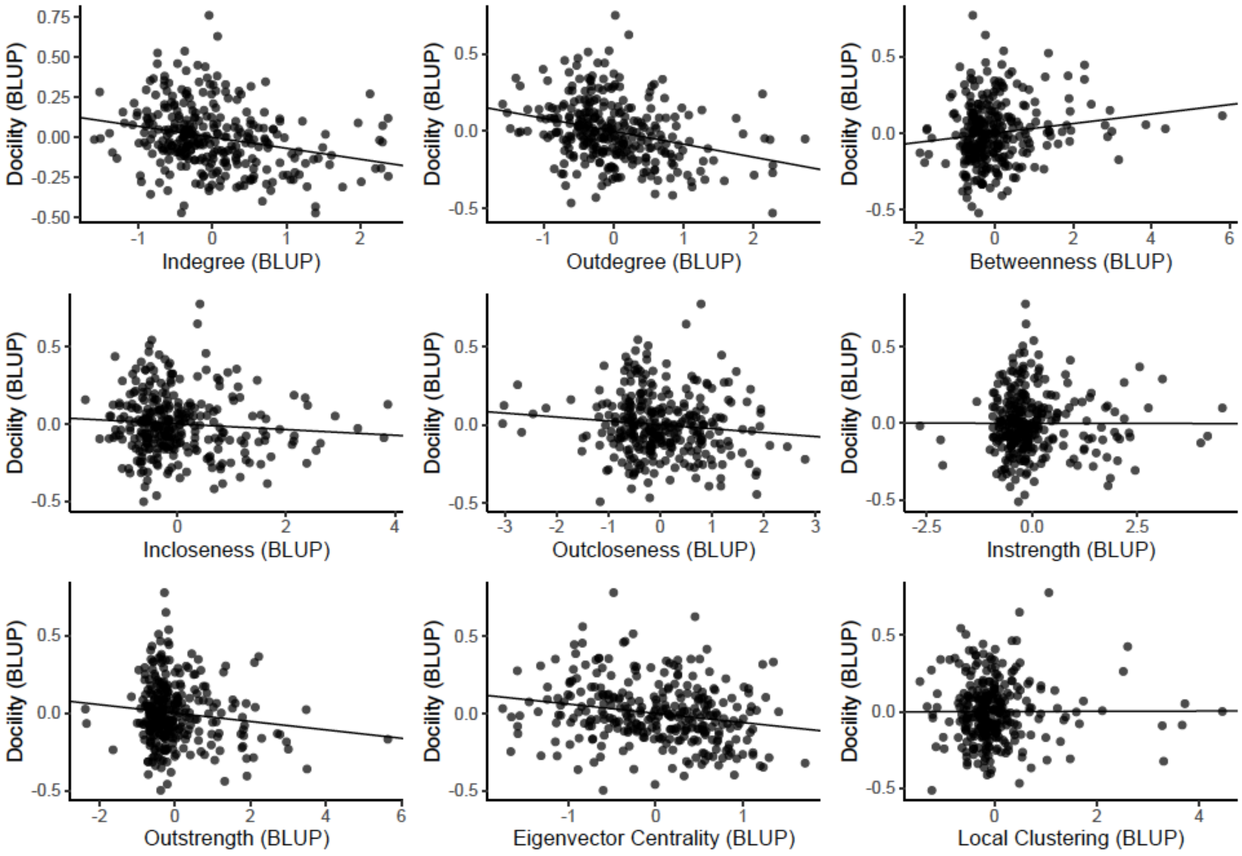

Figure 1.3. Linear regression between best linear unbiased predictions (BLUPs) of affiliative social network traits for each individual and docility. Bold red lines are significantly different from zero according to Table 1.4.

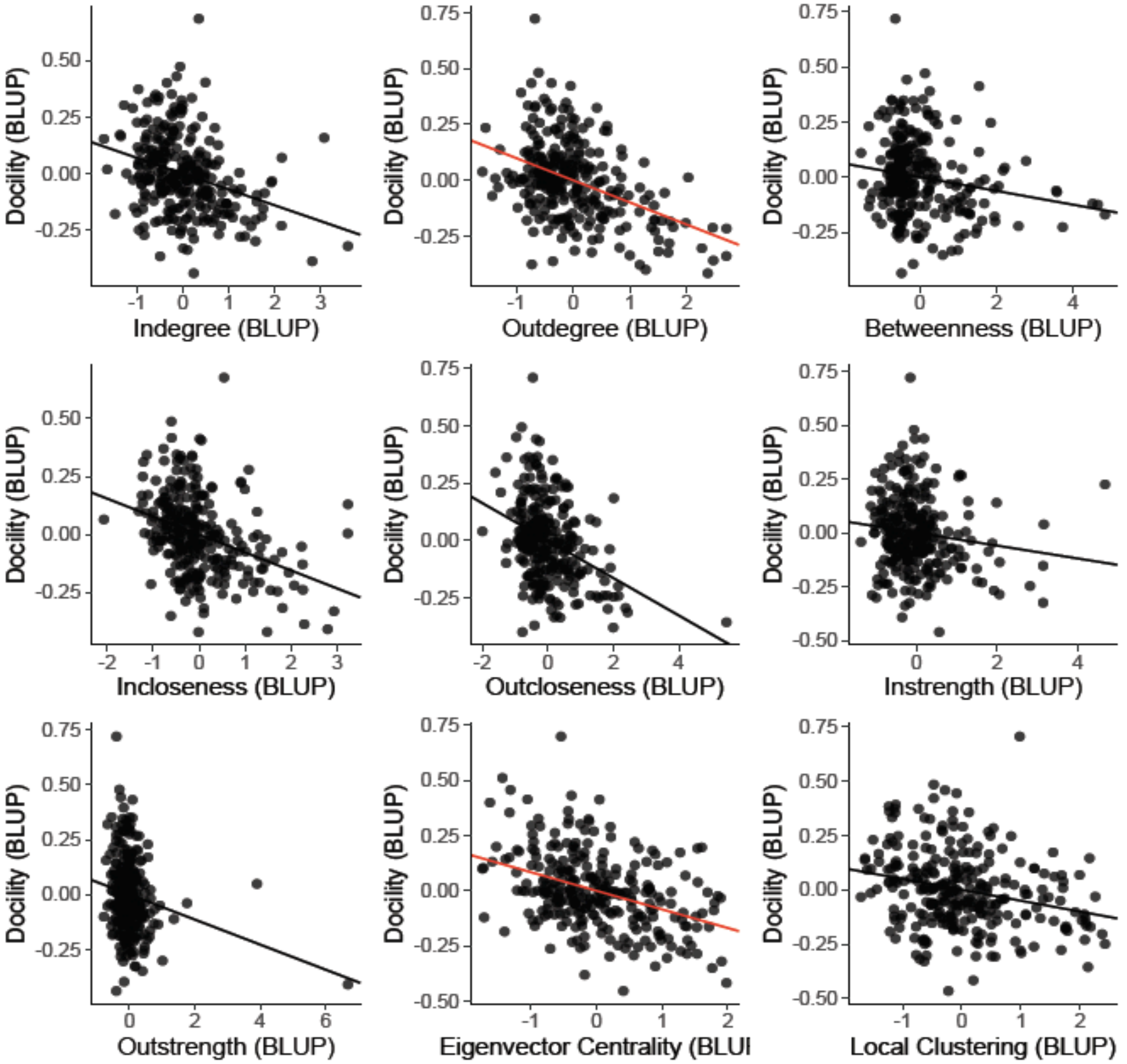

Figure 1.4. Linear regression between best linear unbiased predictions (BLUPs) of agonistic social network traits for each individual and docility. Bold red lines are significantly different from zero according to Table 5.

Tables

Table 1.1. Descriptions of social network measures used in this study.

Social network trait	**Description**
Indegree	Numbers of individuals from whom focal individuals receives interactions (Wasserman and Faust 1994)
Outdegree	Number of individuals with whom focal individuals initiates interactions (Wasserman and Faust 1994)
Incloseness	Focal individual receives interactions more directly from others (Yang et al. 2016)
Outcloseness	Focal individual initiates interactions with others more directly (Yang et al. 2016)
Instrength	Focal individual receives many repeated interactions from others (Wasserman and Faust 1994)

Outstrength	Focal individual initiates many repeated interactions with others (Wasserman and Faust 1994)
Betweenness	Proportion of shortest path lengths that pass through focal individual, i.e., bridging of network (Wey et al. 2008)
Eigenvector centrality	Connectedness of focal individual in network taking into account indirect relationships of neighbors (Wasserman and Faust 1994; Yang et al. 2016)
Local clustering	Cliquishness; embeddedness of focal individual in network (Wey et al. 2008; Mady and Blumstein 2017)

Table 1.2. Results of bivariate models illustrating the among-individual variance of intercepts of social network trait and boldness and correlation at the individual level between boldness and affiliative social network traits. We report the estimate with lower and upper 95% credible intervals between parentheses. Bold results are significantly different from zero.

Social network trait	**V_{SNT}**	**$V_{boldness}$**	**correlation**
Indegree	0.424(0.025/0.60)	0.0004(<0.001/0.001)	-0.233(-0.834/0.663)
Outdegree	0.460(<0.001/0.657)	0.0004(<0.0001/0.001)	-0.260(-0.854/0.622)
Betweenness	1.25(0.847/1.67)	0.0003(<0.001/0.001)	0.015(-0.693/0.787)
Incloseness	0.929(0.624/1.26)	0.0004(<0.001/0.001)	0.123(-0.617/0.872)
Outcloseness	0.794(0.512/1.09)	0.0004(<0.001/0.001)	0.402(-0.555/0.911)
Instrength	0.641(0.453/0.850)	0.0003(<0.001/0.001)	0.105(-0.662/0.806)
Outstrength	0.640(0.451/0.854)	0.0003(<0.001/0.001)	-0.178(-0.820/0.659)
Local clustering	0.590(0.348/0.850)	0.0003(<0.001/0.001)	-0.006(-0.792/0.709)
Eigenvector centrality	0.801(0.545/1.09)	0.0003(<0.001/0.001)	-0.235(-0.812/0.701)

Table 1.3. Results of bivariate models illustrating the among individual variance of intercepts of social network trait and boldness and correlation at the individual level between boldness and agonistic social network traits. We report the estimate with lower and upper 95% credible intervals between parentheses. Bold results are significantly different from zero.

Social network trait	$\mathbf{V_{SNT}}$	$\mathbf{V_{boldness}}$	**correlation**
Indegree	0.915(0.652/1.23)	0.0004(<0.0001/0.002)	-0.073(-0.764/0.700)
Outdegree	0.296(0.178/0.426)	0.0004(<0.0001/0.001)	-0.019(-0.750/0.695)
Betweenness	0.675(0.470/0.899)	0.0006(<0.0001/0.002)	-0.387(-0.929/0.295)
Incloseness	0.848(0.570/1.17)	0.0004(<0.0001/0.002)	-0.028(-0.755/0.741)
Outcloseness	0.402(0.207/0.620)	0.0007(<0.0001/0.002)	-0.542(-0.969/0.251)
Instrength	0.674(0.446/0.928)	0.0005(<0.0001/0.002)	0.244(-0.551/0.851)
Outstrength	0.286(0.178/0.405)	0.0005(<0.0001/0.002)	0.349(-0.385/0.856)
Local clustering	0.956(0.678/1.29)	0.0005(<0.0001/0.002)	0.265(-0.522/0.888)
Eigenvector centrality	0.967(0.632/1.33)	0.0005(<0.0001/0.002)	0.245(-0.500/0.911)

Table 1.4. Results of bivariate models illustrating the variance, covariance and correlation at the individual level between docility and affiliative social network traits. We report the estimate with lower and upper 95% credible intervals between parentheses. Bold results are significantly different from zero.

Social network trait	$\mathbf{V}_{\mathbf{SNT}}$	$\mathbf{V}_{\mathbf{docility}}$	**correlation**
Indegree	0.610(0.503/0.721)	0.107(0.062/0.155)	-0.173(-0.390/0.051)
Outdegree	0.550(0.456/0.644)	0.108(0.060/0.155)	-0.205(-0.409/0.020)
Betweenness	0.711(0.555/0.869)	0.548(0.458/0.634)	0.092(-0.130/0.302)
Incloseness	0.624(0.502/0.772)	0.545(0.457/0.629)	-0.071(-0.267/0.157)
Outcloseness	0.549(0.429/0.679)	0.544(0.446/0.622)	-0.072(-0.282/0.158)
Instrength	0.597(0.474/0.739)	0.547(0.458/0.632)	-0.051(-0.022/0.212)
Outstrength	0.596(0.453/0.722)	0.546(0.462/0.634)	-0.107(-0.293/0.145)
Local clustering	0.517(0.401/0.647)	0.546(0.463/0.633)	0.010(-0.210/0.214)
Eigenvector centrality	0.427(0.323/0.522)	0.548(0.469/0.633)	-0.130(-0.351/0.058)

Table 1.5. Results of bivariate models illustrating the variance, covariance and correlation at the individual level between docility and agonistic social network traits. We report the estimate with lower and upper 95% credible intervals between parentheses. Bold results are significantly different from zero.

Social network trait	V_{SNT}	$V_{docility}$	**correlation**
Indegree	0.675(0.555/0.799)	0.088(0.045/0.132)	-0.194(-0.430/0.028)
Outdegree	0.641(0.528/0.763)	0.089(0.045/0.133)	**-0.274(-0.502/-0.053)**
Betweenness	1.07(0.875/1.27)	0.089(0.047/0.135)	-0.139(-0.345/0.120)
Incloseness	0.717(0.592/0.847)	0.089(0.047/0.133)	-0.226(-0.468/0.209)
Outcloseness	0.715(0.587/0.846)	0.090(0.048/0.135)	-0.253(-0.463/0.003)
Instrength	0.684(0.558/0.806)	0.089(0.048/0.135)	-0.117(-0.291/0.130)
Outstrength	0.406(0.334/0.488)	0.088(0.047/0.135)	-0.114(-0.308/0.071)
Local clustering	0.927(0.756/1.10)	0.093(0.050/0.140)	-0.150(-0.376/0.061)
Eigenvector centrality	0.731(0.598/0.875)	0.086(0.044/0.128)	**-0.248(-0.480/-0.024)**

Table 1.6. Fixed effects fitted on social network measures for the bivariate models of affiliative social network measures and boldness. Yearling was the reference level for age category. Male was the reference level for sex. We report estimate with lower and upper 95% credible intervals between parentheses. Bold values were significantly different from zero.

Social network measure	**SNT: Intercept**	**Age category**	**Sex**	**Yearly predator index**	**Relative Rank**
Indegree	**1.61(1.04/2.23)**	0.033(-0.194/0.261)	0.072(-0.264/0.388)	-0.054(-0.320/0.228)	-0.037(-0.492/0.439)
Outdegree	**1.48(0.895/2.07)**	**0.253(0.020/0.485)**	0.247(-0.094/0.589)	-0.233(-0.509/0.053)	-0.244(-0.725/0.240)
Betweenness	0.825(-0.055/1.69)	**0.523(0.274/0.767)**	0.004(-0.500/0.521)	**-1.15(-1.49/-0.810)**	**-1.09(-1.75/-0.453)**
Incloseness	**0.814(0.043/1.59)**	-0.216(-0.459/0.003)	0.108(-0.343/0.562)	0.189(-0.106/0.501)	0.160(-0.423/0.216)
Outcloseness	0.725(-0.026/1.48)	**0.554(0.283/0.832)**	-0.246(-0.698/0.167)	0.234(-0.119/0.556)	-0.499(-1.13/0.102)
Instrength	**1.54(0.951/2.13)**	**0.359(0.213/0.507)**	-0.069(-0.435/0.284)	0.134(-0.069/0.329)	0.116(-0.323/0.545)
Outstrength	**1.38(0.784/2.01)**	**0.559(0.381/0.741)**	0.176(-0.186/0.544)	-0.037(-0.277/0.205)	0.284(-0.212/0.716)
Local clustering	0.231(-0.536/ 0.976)	-0.005(-0.325/0.298)	-0.266(-0.692/0.134)	-0.103(-0.488/0.277)	0.240(-0.367/0.845)
Eigenvector centrality	**1.10(0.365/1.81)**	**0.287(0.063/0.525)**	**0.151(-0.263/0.583)**	**-0.322(-0.617/-0.023)**	-0.359(-0.934/0.201)

Table 1.7. Fixed effects fitted on boldness for the bivariate models of affiliative social network measures and boldness. Yearling was the reference level for age category. Male was the reference level for sex. We report estimate with lower and upper 95% credible intervals between parentheses. Bold values were significantly different from zero.

Social network measure	**Boldness: Intercept**	**Age category**	**Sex**	**Yearly predator index**	**Relative Rank**	**Days since last event**	**Events per year per colony**	**AmPm**
Indegree	**0.129(0.043/ 0.208)**	0.011(-0.025/ 0.048)	0.016(-0.013/ 0.048)	-0.023(-0.074/ 0.027)	0.0038(-0.048/ 0.052)	-0.0006(-0.002/ -0.0007)	0.0007(-0.0007/ 0.002)	0.003(-0.025/ 0.030)
Outdegree	**0.130(0.049/ 0.212)**	0.010(-0.026/ 0.046)	0.016(-0.014/ 0.048)	-0.024(-0.074/ 0.027)	0.004(-0.046/ 0.052)	-0.0006(-0.002/ 0.0007)	0.0007(-0.0006/ 0.002)	0.003(-0.023/ 0.032)
Betweenness	**0.129(0.048/ 0.208)**	0.011(-0.028/ 0.047)	0.016(-0.014/ 0.047)	-0.024(-0.075/ 0.026)	0.003(-0.049/ 0.051)	-0.0006(-0.002/ 0.0008)	0.0007(-0.0006/ 0.002)	0.003(-0.024/ 0.036)
Incloseness	**0.130(0.047/ 0.210)**	0.009(-0.028/ 0.044)	0.016(-0.014/ 0.047)	-0.024(-0.075/ 0.026)	0.004(-0.043/ 0.055)	-0.0006(-0.002/ 0.0008)	0.0007(-0.0006/ 0.002)	0.003(-0.024/ 0.032)
Outcloseness	**0.129(0.052/ 0.207)**	0.011(-0.025/ 0.045)	0.017(-0.015/ 0.047)	-0.023(-0.119/ 0.556)	0.002(-0.047/ 0.053)	-0.0006(-0.002/ 0.0008)	0.0007(-0.0006/ 0.002)	0.002(-0.027/ 0.029)
Instrength	**0.128(0.048/ 0.211)**	0.010(-0.025/ 0.047)	0.016(-0.013/ 0.048)	-0.021(-0.072/ 0.028)	0.003(-0.047/ 0.053)	-0.0006(-0.002/ 0.0008)	0.0007(-0.0006/ 0.002)	0.003(-0.024/ 0.032)

Outstrength	**0.127(0.044/ 0.205)**	0.010(-0.025/ 0.047)	0.016(-0.015/ 0.046)	-0.023(-0.074/ 0.028)	0.004(-0.043/ 0.056)	-0.0006(-0.002/ 0.0008)	0.0007(-0.0006/ 0.002)	0.003(-0.024/ 0.031)
Local clustering	**0.127(0.047/ 0.209)**	0.011(-0.027/ 0.045)	0.016(-0.015/ 0.047)	-0.023(-0.074/ 0.027)	0.003(-0.046/ 0.052)	-0.0006(-0.002/ 0.0008)	0.0007(-0.0005/ 0.002)	0.003(-0.024/ 0.032)
Eigenvector centrality	**0.128(0.045/ 0.207)**	0.010(-0.025/ 0.046)	0.016(-0.014/ 0.046)	-0.023(-0.073/ 0.028)	0.005(-0.044/ 0.054)	-0.0006(-0.002/ 0.0008)	0.0007(-0.0006/ 0.002)	0.003(-0.024/ 0.032)

	Alert distance	**Burrow distance**
Indegree	**-0.0008(-0.001/-0.0003)**	-0.0007(-0.002/0.0008)
Outdegree	**-0.0008(-0.001/-0.0002)**	-0.0007(-0.002/0.0007)
Betweenness	**-0.0008(-0.001/-0.0002)**	-0.0006(-0.002/0.0007)
Incloseness	**-0.0008(-0.0001/-0.0003)**	-0.0006(-0.002/0.0008)
Outcloseness	**-0.0008(-0.0001/-0.0002)**	-0.0006(-0.002/0.0007)
Instrength	**-0.0008(-0.001/-0.0003)**	-0.0006(-0.002/0.0007)
Outstrength	**-0.0008(-0.001/-0.0003)**	-0.0006(-0.002/0.0008)
Local clustering	**-0.0008(-0.001/-0.0003)**	-0.0006(-0.002/0.0008)
Eigenvector centrality	**-0.0008(-0.001/-0.0002)**	-0.0006(-0.002/0.0008)

Table 1.8. Fixed effects fitted on social network measures within bivariate models of agonistic social network measures and boldness. Yearling was the reference level for age category. Male was the reference level for sex. We report estimate with lower and upper 95% credible intervals between parentheses. Bold values were significantly different from zero.

Social network measure	**SNT: Intercept**	**Age category**	**Sex**	**Yearly predator index**	**Relative Rank**
Indegree	-0.446(-1.14/ 0.235)	**-0.345(-0.495/-0.204)**	-0.210(-0.632/0.241)	**1.05(0.844/1.25)**	**0.675(0.143/1.17)**
Outdegree	**1.65(1.15/2.21)**	**-0.801(-1.00/-0.586)**	**0.445(0.158/0.741)**	**-0.343(-0.601/-0.092)**	**-0.520(-0.934/-0.105)**
Betweenness	0.006(-0.658/0.637)	**-0.677(-0.881/-0.472)**	0.110(-0.276/0.518)	**0.449(0.183/0.700)**	0.323(-0.198/0.844)
Incloseness	**0.766(0.017/1.50)**	-0.101(-0.342/0.120)	-0.281(-0.754/0.160)	0.606(0.311/0.923)	0.245(-0.362/0.053)
Outcloseness	**1.73(1.10/2.42)**	**-0.534(-0.810/-0.256)**	-0.037(-0.038/0.033)	-0.230(-0.564/0.098)	-0.255(-0.764/0.051)
Instrength	-0.454(-1.09/ 0.202)	**-1.06(-1.260/-0.858)**	-0.024(-0.420/0.353)	**0.932(0.676/1.17)**	**1.52(0.983/2.047)**
Outstrength	0.472(-0.107/1.03)	**-0.638(-0.892/-0.390)**	**0.413(0.096/0.722)**	0.108(-0.184/0.409)	0.264(-0.419/0.498)
Local clustering	0.077(-0.650/ 0.782)	**0.377(0.205/0.549)**	-0.199(-0.633/0.262)	-0.706(-0.936/-0.475)	0.494(-0.087/1.02)
Eigenvector centrality	0.515(-0.293/1.28)	0.163(-0.088/0.409)	0.313(-0.147/0.790)	**-0.374(-0.683/-0.058)**	**-1.25(-1.91/-0.611)**

Table 1.9. Fixed effects fitted on boldness within bivariate models of agonistic social network measures and boldness. Yearling was the reference level for age category. Male was the reference level for sex. We report estimate with lower and upper 95% credible intervals between parentheses. Bold values were significantly different from zero.

Social network measure	**Boldness: Intercept**	**Age category**	**Sex**	**Yearly predator index**	**Relative Rank**	**Days since last event**	**Events per year per colony**	**AmPm**
Indegree	**0.134(0.047/ 0.217)**	0.012(-0.023/ 0.047)	0.009(-0.021/ 0.040)	-0.011(-0.064/ 0.041)	0.006(-0.042/ 0.053)	-0.0004(-0.002/ 0.001)	0.0001(-0.001/ 0.002)	0.003(-0.024/ 0.030)
Outdegree	**0.134(0.051/ 0.216)**	0.012(-0.023/ 0.049)	0.008(-0.022/ 0.040)	-0.011(-0.063/ 0.040)	0.006(-0.042/ 0.054)	-0.0004(-0.002/ 0.001)	0.0001(-0.001/ 0.001)	0.003(-0.025/ 0.031)
Betweenness	**0.146(0.059/ 0.231)**	0.016(-0.019/ 0.055)	0.009(-0.022/ 0.040)	-0.013(-0.065/ 0.037)	0.004(-0.046/ 0.055)	-0.0004(-0.002/ 0.0009)	-0.0001(-0.002/ 0.001)	0.003(-0.025/ 0.031)
Incloseness	**0.135(0.050/ 0.217)**	0.012(-0.025/ 0.047)	0.009(-0.021/ 0.041)	-0.011(-0.063/ 0.040)	0.006(-0.043/ 0.053)	-0.0004(-0.002/ 0.001)	0.0001(-0.001/ 0.001)	0.003(-0.024/ 0.031)
Outcloseness	**0.133(0.048/ 0.218)**	0.017(-0.021/ 0.054)	0.007(-0.026/ 0.039)	-0.008(-0.061/ 0.044)	0.003(-0.049/ 0.051)	-0.0004(-0.002/ 0.001)	0.0001(-0.001/ 0.002)	0.003(-0.024/ 0.030)
Instrength	**0.135(0.054/ 0.223)**	0.009(-0.029/ 0.046)	0.009(-0.023/ 0.040)	**0.933(0.676/ 1.17)**	0.009(-0.040/ 0.056)	-0.0004(-0.002/ 0.001)	0.0001(-0.001/ 0.002)	0.003(-0.024/ 0.030)

Outstrength	**0.135(0.053/ 0.221)**	0.015(-0.023/ 0.050)	0.007(-0.025/ 0.038)	-0.011(-0.063/ 0.042)	0.005(-0.045/ 0.053)	-0.0004(-0.002/ 0.001)	0.0001(-0.001/ 0.001)	0.003(-0.024/ 0.030)
Local clustering	0.077(-0.650/ 0.782)	0.012(-0.022/ 0.048)	0.009(-0.022/ 0.040)	-0.013(-0.066/ 0.039)	0.006(-0.042/ 0.055)	-0.0004(-0.002/ 0.0009)	0.0001(-0.001/ 0.001)	0.003(-0.026/ 0.030)
Eigenvector centrality	**0.131(0.043/ 0.210)**	0.015(-0.020/ 0.054)	0.008(-0.023/ 0.040)	-0.013(-0.065/ 0.039)	0.002(-0.051/ 0.049)	-0.0004(-0.002/ 0.001)	0.0003(-0.001/ 0.002)	0.003(-0.023/ 0.031)

Social network measure	**Alert distance**	**Burrow distance**
Indegree	**-0.0009(-0.001/-0.0003)**	-0.0006(-0.002/0.0008)
Outdegree	**-0.0009(-0.001/-0.0003)**	-0.0006(-0.002/0.0008)
Betweenness	**-0.0009(-0.001/-0.0003)**	-0.0006(-0.002/0.0009)
Incloseness	**-0.0009(-0.001/-0.0003)**	-0.0006(-0.002/0.0008)
Outcloseness	**-0.0009(-0.001/-0.0003)**	-0.0006(-0.002/0.0007)
Instrength	**-0.0008(-0.001/-0.0003)**	-0.0005(-0.002/0.0009)
Outstrength	**-0.0009(-0.001/-0.0003)**	-0.0005(-0.002/0.0008)
Local clustering	**-0.0008(-0.001/-0.0002)**	-0.0005(-0.002/0.0008)
Eigenvector centrality	**-0.0008(-0.001/-0.0003)**	-0.0005(-0.002/0.0008)

Table 1.10. Fixed effects fitted on social network measures for the bivariate models of affiliative social network measures and docility Yearling was the reference level for age category. Male was the reference level for sex. We report estimate with lower and upper 95% credible intervals between parentheses. Bold values were significantly different from zero.

Social network measure	**SNT: Intercept**	**Age category**	**Sex**	**Yearly predator index**	**Relative Rank**
Indegree	**1.66(1.22/2.11)**	0.265(0.213/0.318)	-0.082(-0.264/0.097)	**0.218(0.137/0.298)**	**0.442(0.334/0.563)**
Outdegree	**1.60(1.17/2.03)**	**0.225(0.170/0.285)**	**0.172(0.002/0.356)**	0.167(0.085/0255)	**0.221(0.092/0.338)**
Betweenness	**0.692(0.119/1.30)**	**-0.369(-0.459/-0.280)**	-0.080(-0.322/0.158)	**-0.182(-0.314/-0.049)**	**0.195(0.002/0.389)**
Incloseness	**0.824(0.327/1.39)**	0.084(0.021/0.151)	0.004(-0.209/0.219)	**0.343(0.244/0.439)**	**-0.323(-0.462/-0.184)**
Outcloseness	0.387(-0.162/ 0.902)	**0.191(0.112/0.265)**	-0.060(-0.280/0.157)	**0.648(0.533/0.763)**	**-0.446(-0.614/-0.287)**
Instrength	**2.07(1.54/2.58)**	**0.219(0.179/0.261)**	-0.084(-0.292/0.127)	0.160(-0.095/0.226)	**0.125(0.030/0.221)**
Outstrength	**2.13(1.63/2.67)**	**0.114(0.075/0.155)**	**0.229(0.008/0.435)**	**0.109(0.047/0.171)**	**0.128(0.039/0.219)**
Local clustering	-0.199(-0.708/ 0.302)	**0.247(0.148/0.351)**	-0.083(-0.285/0.127)	-0.066(-0.209/0.086)	-0.093(-0.307/0.112)
Eigenvector centrality	**0.615(0.145/1.06)**	**0.568(0.483/0.650)**	0.007(-0.182/0.194)	**-0.317(-0.440/-0.198)**	**0.651(0.471/0.825)**

Table 1.11. Fixed effects fitted on docility within bivariate models of affiliative social network measures and docility. Yearling was the reference level for age category. Male was the reference level for sex. We report estimate with lower and upper 95% credible intervals between parentheses. Bold values were significantly different from zero.

Social network measure	**Docility: Intercept**	**Age category**	**Sex**	**Yearly predator index**	**Relative Rank**	**Days since last event**	**Events per year per colony**	**AmPm**
Indegree	**1.64(1.29/ 2.00)**	-0.003(-0.124/ 0.115)	0.084(-0.042/ 0.213)	0.102(-0.076/ 0.275)	**0.251(0.064/ 0.437)**	**0.007(0.003/ 0.010)**	**-0.001 (-0.002/ -0.0002)**	-0.078(-0.162/ 0.008)
Outdegree	**1.64(1.28/ 2.01)**	-0.0008(-0.124/ 0.114)	0.084(-0.043/ 0.210)	0.010(-0.065/ 0.278)	**0.258(0.070/ 0.443)**	**0.007(0.003/ 0.010)**	**-0.001 (-0.003/ -0.0002)**	-0.078(-0.163/ 0.008)
Betweenness	**1.62(1.27/ 2.01)**	**-0.024(-0.143/ -0.094)**	0.082(-0.0422/ 0.210)	-0.110(-0.064/ 0.284)	**0.285(0.099/ 0.473)**	**0.007(0.003/ 0.010)**	-0.001 (-0.002/ 0.0008)	-0.076(-0.159/ 0.010)
Incloseness	**1.62(1.26/ 1.98)**	-0.017(-0.136/ 0.100)	0.082(-0.046/ 0.212)	**0.110(-0.067/ -0.276)**	**0.280(0.091/ 0.464)**	**0.007(0.003/ 0.010)**	**-0.001 (-0.002/ -0.00002)**	-0.076(-0.158/ 0.008)

Outcloseness	**1.62(1.26/1.97)**	-0.017(-0.131/0.105)	0.081(-0.051/0.204)	0.107(-0.061/0.291)	**0.283(0.090/0.467)**	**0.007(0.003/0.01)**	**-0.001 (-0.002/-0.00008)**	-0.077(-0.160/0.006)
Instrength	**1.62(1.25/2.57)**	-0.019(-0.133/0.105)	0.084(-0.045/0.209)	-0.111(-0.070/0.285)	**0.279(0.091/0.465)**	**0.007(0.003/0.010)**	**-0.001 (-0.002/0.000005)**	-0.077(-0.158/0.009)
Outstrength	**1.62(1.25/1.98)**	**-0.016(-0.135/-0.104)**	0.008(-0.044/0.207)	0.105(-0.006/0.029)	**0.279(0.091/0.457)**	**0.007(0.003/0.010)**	**-0.001 (-0.002/-0.00004)**	-0.079(-0.160/0.079)
Local clustering	**1.62(1.26/1.97)**	-0.019(-0.133/0.103)	0.083(-0.050/0.206)	-0.111(-0.068/0.282)	**0.278(0.091/0.457)**	**0.007(0.003/0.010)**	-0.001 (-0.002/0.00007)	-0.077(-0.164/0.005)
Eigenvector centrality	**1.62(1.29/1.99)**	-0.013(-0.133/0.103)	0.084(-0.385/0.213)	**0.121(-0.058/0.289)**	**0.246(0.058/0.437)**	**0.007(0.003/0.010)**	**-0.001 (-0.002/-0.00009)**	-0.078(-0.167/0.002)

Table 1.12. Fixed effects fitted on social network measures for the bivariate models of agonistic social network measures and docility. Yearling was the reference level for age category. Male was the reference level for sex. We report estimate with lower and upper 95% credible intervals between parentheses. Bold values were significantly different from zero.

Social network measure	**SNT: Intercept**	**Age category**	**Sex**	**Yearly predator index**	**Relative Rank**
Indegree	**0.538(0.063/1.00)**	**-0.078(-0.143/-0.012)**	-0.047(-0.253/0.156)	0.236(0.126/0.339)	**1.08(0.928/1.21)**
Outdegree	**2.43(1.97/2.87)**	**-0.711(-0.772/-0.654)**	**0.315(0.128/0.524)**	**-0.196(-0.294/-0.099)**	**-0.494(-0.630/-0.368)**
Betweenness	**1.10(0.509/1.70)**	**-0.205(-0.281/-0.123)**	0.044(-0.218/0.298)	-0.067(-0.196/0.062)	**-0.373(-0.552/-0.205)**
Incloseness	**1.380(0.886/1.86)**	**-0.184(-0.237/-0.132)**	0.134(-0.070/0.340)	0.066(-0.018/0.154)	**0.747(0.632/0.863)**
Outcloseness	**2.88(2.38/3.35)**	**-0.375(-0.435/-0.315)**	-0.013(-0.222/0.191)	**-0.464(-0.559/-0.364)**	**-0.179(-0.308/-0.041)**
Instrength	0.383(-0.098/ 0.874)	**-0.314(-0.384/-0.244)**	-0.091(-0.303/0.113)	**0.217(0.103/0.330)**	**0.944(0.794/1.10)**
Outstrength	**0.950(0.549/1.34)**	**-0.604(-0.687/-0.525)**	0.309(0.138/0.472)	**0.055(-0.077/0.173)**	-0.077(-0.249/0.090)
Local clustering	-0.268(-0.849/0.269)	**0.431(0.354/0.513)**	-0.041(-0.281/0.205)	-0.097(-0.224/0.033)	0.045(-0.136/0.213)
Eigenvector centrality	**0.616(0.122/1.10)**	**-0.403(-0.479/-0.329)**	0.061(-0.157/0.274)	-0.379(-0.497/-0.253)	**0.626(0.463/0.795)**

Table 1.13. Fixed effects fitted on docility for the bivariate models of agonistic social network measures and docility Yearling was the reference level for age category. Male was the reference level for sex. We report estimate with lower and upper 95% credible intervals between parentheses. Bold values were significantly different from zero.

Social network measure	**Docility: Intercept**	**Age category**	**Sex**	**Yearly predator index**	**Relative Rank**	**Days since last event**	**Events per year per colony**	**AmPm**
Indegree	**1.70(1.34/ 2.09)**	**-0.061(-0.184/ 0.069)**	0.098(-0.033/ 0.227)	0.124(-0.073/ 0.309)	**0.262(0.075/ 0.463)**	**0.007(0.003/ 0.011)**	**-0.001(-0.003/ -0.0004)**	-0.071(-0.159/ 0.017)
Outdegree	**1.66(1.31/ 2.05)**	-0.076(-0.204/ 0.049)	0.100(-0.032/ 0.228)	0.148(-0.052/ 0.339)	**0.316(0.126/ 0.508)**	**0.007(0.004/ 0.011)**	**-0.002(-0.003/-0.0004)**	-0.071(-0.157/ 0.020)
Betweenness	**1.70(1.32/ 2.08)**	-0.079(-0.209/ 0.420)	0.105(-0.022/ 0.233)	0.125(-0.063/ 0.326)	**0.301(0.010/ 0.489)**	**0.007(0.003/ 0.011)**	**-0.001(-0.003/-0.0002)**	-0.072(-0.158/ 0.019)
Incloseness	**1.69(1.32/ 2.07)**	-0.054(-0.187/ 0.073)	0.093(-0.033/ 0.230)	0.126(-0.074/ 0.314)	**0.261(0.070/ 0.454)**	**0.007(0.003/ 0.011)**	**-0.002(-0.003/-0.0004)**	-0.07(-0.160/ 0.017)
Outcloseness	**1.64(1.26/ 2.02)**	-0.069(-0.198/ 0.054)	0.096(-0.034/ 0.229)	0.161(-0.039/ 0.358)	**0.296(0.101/ 0.492)**	**0.007(0.003/ 0.011)**	**-0.002(-0.003/-0.0004)**	-0.072(-0.165/ 0.016)
Instrength	**1.67(1.31/ 2.06)**	**-0.072(-0.196/ 0.057)**	0.099(-0.030/ 0.230)	0.129(-0.063/ 0.321)	**0.284(0.098/ 0.478)**	**0.007(0.003/ 0.011)**	**-0.001(-0.002/-0.0001)**	-0.071(-0.157/ 0.020)

Outstrength	**1.67(1.31/2.05)**	-0.086(-0.215/0.043)	0.106(-0.027/0.237)	0.132(-0.055/0.328)	**0.294(0.099/0.485)**	**0.007(0.003/0.011)**	**-0.001(-0.002/-0.0001)**	-0.072(-0.165/0.014)
Local clustering	**1.68(1.31/2.07)**	-0.080(-0.207/0.046)	0.098(-0.037/0.226)	0.120(-0.072/0.315)	**0.294(0.102/0.486)**	**0.007(0.003/0.011)**	**-0.001(-0.002/-0.0005)**	-0.07(-0.159/0.018)
Eigenvector centrality	**1.68(1.28/2.04)**	-0.077(-0.198/0.052)	0.101(-0.034/0.225)	0.163(-0.032/0.362)	**0.264(0.078/0.460)**	**0.007(0.004/0.011)**	**-0.002(-0.003/-0.0004)**	-0.071(-0.157/0.021)

Chapter 3: Social position indirectly influences the traits yellow-bellied marmots use to solve problems

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ORIGINAL PAPER

Social position indirectly influences the traits yellow-bellied marmots use to solve problems

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Abstract

Animals adapt to changing environments by behaving flexibly when solving problems. Traits, such as sex and age, and specifically behavioral traits like persistence–the amount of time spent attempting to solve a problem, are positively associated with successful problem-solving. However, individuals face social pressures, such as aggression, which may directly alter an individual's behavior or interact with sex or age, when they attempt to problem-solve. We examined the direct and indirect effects of social position and individual behavioral traits on solving a novel puzzle box in facultatively social yellow-bellied marmots (*Marmota flaviventer*), using both generalized linear mixed models and confirmatory path analysis. We found strong support that marmots who used a diversity of behaviors were more successful problem-solvers and weak support that those who received more aggression were less successful. Additionally, marmots who received more aggression were less behaviorally diverse, less behaviorally selective and less persistent while trying to open the puzzle box. Thus, we show that aggression indirectly decreases problem-solving success by acting on the behavioral traits that an individual uses. We conclude that specific social relationships, including the type of interaction and whether they are recipients or initiators, influences the ways in which an individual interacts with cognitive tests and should be considered in analysis of individual problem-solving.

Keywords Social networks · Structural equation modeling · Yellow-bellied marmots · Problem-solving · Cognition · innovation

Background

Animals encounter numerous novel physical or social environments throughout their lives that may be due to dispersal, migration, social upheavals or catastrophic environmental events. To prosper, individuals must be able to flexibly adjust to these novel environments. Innovation, or problem-solving, is one way by which animals are able to adapt to these changes. Innovation is the ability to devise a novel solution to a novel or existing problem (Reader and Laland 2003) and this ability often carries fitness benefits. Birds with larger brain size, a correlate of innovation, are better at establishing populations in novel environments (Sol et al. 2005a). In Palearctic birds, innovation allows overwinter residents to utilize novel food sources, a skill that their migratory counterparts lack (Sol et al. 2005b). 'Nuisance' species, such as racoons (*Procyon lotor*), are enthusiastic problem-solvers, a skill that seems to aid them in the settlement of human-altered habitats and sometimes bring them into conflict with humans (Barrett et al. 2019). With human impacts rapidly altering environments physically, chemically and behaviorally (e.g., Sih et al. 2016), there is an increasing need to understand which animals will be able to behaviorally adapt to these challenges and how they will do so.

Problem-solving ability varies greatly across species (chimpanzees *Pan troglodytes* Reader and Laland 2001; black-throated monitor lizards *Varanus albigularis albigularis* Manrod et al. 2008; spotted hyenas *Crocuta crocuta* Benson-Amram and Holekamp 2012) and individuals (Johnson-Ulrich et al. 2020; Rowell and Rymar 2019). Innovation and problem-solving are difficult to study in the wild as they require a breadth of knowledge on a species behavior.

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Instead, many researchers study problem-solving through the introduction of novel tasks, such as puzzle boxes (Griffin and Guez 2014). These puzzle boxes have helped researchers experimentally test why these variations arise. Across species, traits like brain size (Benson-Amram et al. 2016) and being a habitat generalist (Overington et al. 2011) seem to drive problem-solving ability. Some life history traits, such as age, where older individuals are more likely to innovate (Kendal et al. 2005), or dominance rank, where lower-ranked individuals lack access to normal food sources and are forced to innovate (Thornton and Samson 2012) may correlate with individual variation. However, individual variation is most frequently predicted by behavioral traits, defined by their consistency—which may be traits such as persistence or personality traits such as boldness (Amici et al. 2019). The relationships between problem-solving and some behavioral traits are straightforward. *Neophobia*, defined as an aversion to new stimuli, may compromise an animal's ability to problem-solve by preventing them from interacting with a novel object (Benson-Amram and Holekamp 2012; Benson-Amram et al. 2013). By contrast, *persistence*, defined as engaging in multiple attempts or spending more time trying to solve a puzzle, is frequently associated with problem-solving success with more persistent individuals being more successful (Keagy et al. 2009; Overington et al. 2011; Thornton and Samson 2012; Benson-Amram and Holekamp 2012; Cole et al. 2012; Chow et al. 2016; Loepelt et al. 2016). Similarly, individuals who attempt a large number of behaviors, referred to as being exploratory or engaging in *behavioral diversity*, are more likely to generate an innovative solution to a problem (Benson-Amram et al. 2013; Griffin et al. 2014; Griffin and Diquelou 2015; Daniels et al. 2019) because they are able to gather more information about an object (Reader and Laland 2003). The relationship between problem-solving and other behavioral traits is less clear-cut. *Behavioral selectivity*, engaging in behaviors most likely to successfully solve a problem, such as manipulating a handle to release a door rather than chewing on the bottom, minimizes energy and opportunity costs of problem-solving by engaging in efficient activities (Benson-Amram and Holekamp 2012; Chow et al. 2016; Daniels et al. 2019). Behavioral selectivity, however, requires trade-offs so that an individual cannot have both high behavioral diversity and high behavioral selectivity (Chow et al. 2016). The question is then, what drives individuals to use different behavioral traits when they solve a problem?

Context is often important to understand an individuals' decision-making and problem-solving and is likely influenced by an individuals' life history and current physiological, environmental and social circumstances (Boogert et al. 2018). Captive pack-living dogs (*Canis familiaris*) and pet dogs were more persistent and manipulative when interacting with a puzzle solving task than were free-ranging dogs. Free-ranging dogs lack a consistent food source and were likely less persistent as a means of conserving energy. Additionally, captive and pet dogs live in an environment where humans encourage and reward interaction with novel objects, which may increase both their motivation and persistence (Lazzaroni et al. 2019). In spotted hyenas (*Crocuta crocuta*), captive individuals had greater initial exploratory behavior and lower neophobia, making them better puzzle solvers than their wild counterparts (Benson-Amram et al. 2013). Subordinate black-capped chickadees (*Poecile atricapillus*) were more successful problem-solvers because dominant individuals guard easily accessible food resources, forcing subordinates to forage on more difficult to access resources. Subordinates subsequently also exhibited less neophobia (MacDougall-Shackleton et al. 2011). Thus, different physical or social environments alter the behaviors that individuals use when confronted with novel problems and, in turn, these changes can alter their problem-solving success.

The interaction of the physical/social environment and behavior is, however, complex and may involve multiple simultaneous interacting factors as well as both indirect and direct effects. This is particularly true for an individuals' social interactions, which can include hierarchies, different styles of relationships and indirect influences from the broader group. Social networks (Wey et al. 2008) quantitatively measure all of an individual's relationships with other members of their group and can be analyzed to extract information such as how many individuals a focal individual interacts with or how much influence they hold over the rest of the group. While most prior studies of social influences of problem-solving focused on dominance rank, social networks allow for more precise questions to be asked about how measures of an individuals' position in their social network might influence their behavior. Additionally, an individuals' social network may influence problem-solving in both direct and indirect ways. Directly, an individuals' social network position may determine how much information about the task they have access to through their close contacts or whether they are targets of aggression and thus, have increased motivation to open the box. An individuals' social network position may also influence which behavioral trait they are most likely to use. For example, an individual who is a frequent target of aggression may not be very persistent while attempting to solve the box. These complex multivariate interactions can be modeled with structural equation modeling, which accounts for the indirect and direct effects of multiple factors on a single outcome (Shipley 2000).

Here, we sought a more comprehensive understanding of how social factors and behavioral traits influence problem-solving success at a novel puzzle box in yellow-bellied marmots (*Marmota flaviventer*). To do this, we adopted a multistep approach using both correlative analyses and causal confirmatory path analysis to account for both direct and indirect pathways to successful problem solving. We first tested for associations between our 11 factors (four behavioral traits measured from interactions with a puzzle box: behavioral diversity, behavioral selectivity, neophobia and persistence, and six social measures: three affiliative PCAs, three agonistic PCAs and relative dominance rank) and problem-solving success using generalized linear mixed effects models and general linear models (summarized in Fig. 1a). We then used confirmatory path analysis (Shipley 2000) to test 24 hypothesized causal path diagrams of how social factors directly and indirectly effect problem-solving success via behavioral trait (summarized in Fig. 1b). We hypothesized that individuals with different social measures would use different behavioral traits to successfully solve the novel puzzle box.

Yellow-bellied marmots are a facultatively social, hibernating rodent species that have been studied at the Rocky Mountain Biological Laboratory since 1962 (Armitage 2014). While rodents are frequently used in cognition research, innovation and problem-solving have never been studied within the genus *Marmota*. Marmots are generalist herbivores that do not typically engage in extractive foraging (Armitage 2014), although they do occasionally manipulate objects in their environment (i.e., moving rocks, playing with sticks, pers. obs.). Problem-solving ability is often tested in species that regularly engage in extractive foraging, yet we believe that 'absence of evidence is not evidence of absence', and marmots permit us to test whether these problem-solving abilities exist, and indeed operate in similar ways in species that may not have an immediate benefit from them.

Additionally, marmots have a wide range of social structures available to be studied within a single population which makes them particularly suitable to test our question of the indirect effects of social networks on problem-solving. Marmots live in harem-polygynous matrilineal colonies composed of one to several related females, their pups, yearlings and one to two dominant males (Blumstein 2013; Armitage 2014). Considerable prior work has shown that, in contrast to many species, yellow-bellied marmots suffer costs of engaging in affiliative behavior and receive some benefits from agonistic behavior. Affiliative social measures are frequently associated with negative fitness outcomes, including individuals with stronger affiliative relationships were more likely to die during hibernation (Yang et al. 2016), live shorter lives (Blumstein et al. 2018) and suffer decreased reproductive success (Wey and Blumstein 2012). Additionally, individuals with more affiliative interaction partners, who had fewer degrees of separation from others in their affiliative network, died younger (Blumstein et al. 2018). Yearling females seem to be the only ones to benefit from strong affiliative relationships, which may protect them from predators (Montero et al. 2020). Meanwhile, males who are more aggressive towards others have higher reproductive success (Wey and Blumstein 2012). Females become more agonistic with age (Wey and Blumstein 2010), which can serve to reproductively suppress younger females and

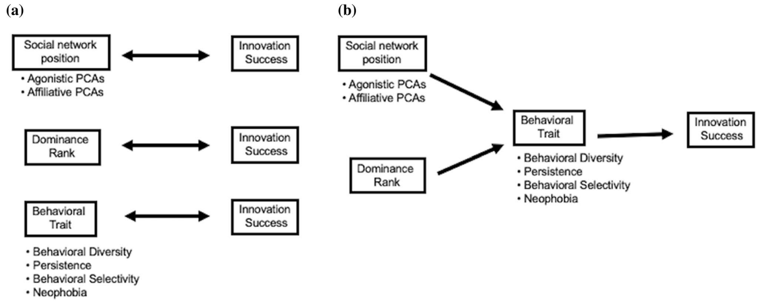

Fig. 1 Illustration of alternative model fitting approaches. **a** Correlative model testing the association between 12 different traits and problem-solving success. Traits have been consolidated into three categories for clarity: behavioral traits (four strategies: behavioral diversity, behavioral selectivity, persistence, and neophobia), social measures (three affiliative PCAs and three agonistic PCAs outlined in Tables 2 and 3) and dominance rank (measured as relative rank). **b** Causal model (SEM) testing the hypothesized link between social position (controlling for dominance) and problem-solving success mediated by behavioral trait. Traits have been consolidated into three categories for clarity (see above for descriptions). All possible combinations of these traits were tested in a series of twenty-eight separate models

concentrate resources for an aggressive females' offspring (Armitage 1991, 2003). Social dominance in pups correlates with higher dominance rank as adults (Huang et al. 2011), which is also correlated with higher body mass (a key factor associated with reproductive success) (Huang et al. 2011). This interesting pattern of negative affiliative relationships and some positive agonistic relationships allows us to test whether sociality affects problem-solving differently in species with less frequent social interactions where affiliative relationships, typically important to problem-solving, are costly.

Materials and methods

Study site and system

We presented puzzle boxes to yellow-bellied marmots at eight colony sites in and around the Rocky Mountain Biological Laboratory located in Gothic, CO. Each colony was a geographically distinct area (colony size range: 2–44 individuals, average: 21 individuals) that contained one or more social groups, which were socially isolated groups of interacting individuals within a colony. Colonies ranged from 0.52 km (the two nearest colonies) to 5 km apart (colonies at the opposite ends of the valley) and while marmots can travel this distance, dispersal from one colony to another is rare. We observed no inter-colony movement during this study period. These marmots are part of a long-term study (Blumstein 2013; Armitage 2014) and individuals are regularly trapped and individually marked with numbered ear tags and unique pictograms are dyed on their dorsal pelage for identification from afar (Blumstein et al. 2009). Observers use binoculars and 15–45 × spotting scopes to record social interactions with all occurrence behavioral sampling. Recorded behaviors follow a defined ethogram of affiliative (sit together, play, greet, allogroom, follow, forage together) and agonistic (aggressive bite, box, chase, grab/slap/push, mouth spar, pounce, snap/snarl/hiss, displacement) behaviors (full ethogram with descriptions in Table 1 in Online Resource 1). Observers are positioned at distances chosen so as to not interfere with normal behavior (Blumstein et al. 2009). Social interactions were recorded from mid-April, when marmots emerge, until mid-September when they begin to enter hibernation. During this period, behavioral observations are conducted on most days, weather permitting, during hours of peak activity (7–10 h in the morning and 16–19 h in the afternoon, (Blumstein et al. 2009).

Puzzle box

We constructed and deployed eight, wood-framed, plexiglass puzzle boxes (30.84 × 30.84 × 30.84 cm, Fig. 2). Each box had two hinged sides that an individual could interact with and open to obtain food. The first solution was the lid of the box, which had a plexiglass protrusion, and marmots could use any part of their body to lift the lid by the protrusion or by gripping the lid itself and pushing it up. The second solution was a door on one side of the box, which marmots could use any part of their body to pull open. Both solutions were held shut by two 5.08 cm Velcro strips placed on either side of the plexiglass projection (lid) or a small metal knob (door) (Video of solutions provided in Online Resource 2). The solutions were designed so that the behaviors required to open the boxes were already in the marmots' repertoires (i.e., pushing and pulling objects, manipulating objects with their mouths). A marmot was considered to have 'successfully innovated' if they approached a closed puzzle box and

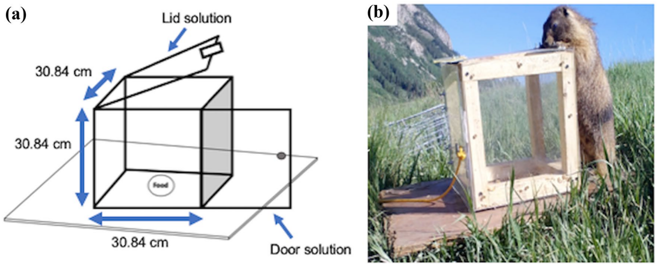

Fig. 2 Puzzle box. **a** Diagram of experimental puzzle box. The puzzle box is made of a 30.84×30.84×30.84 cm wooden frame covered in plexiglass with a hinged door and hinged lid to provide access. The whole apparatus was affixed to a piece of plywood to prevent the box from being flipped. Not marked: The plywood base is 60.7×50.8 cm. **b** Photograph of actual puzzle box

proceeded to open it using either of the two solutions and obtained the food inside, which was determined by seeing them chewing or eating. Although both box solutions were given equal resistance, the marmots overwhelmingly preferred the lid solution, which may reflect that marmots are used to pushing objects with their nose rather than pulling or that marmots may have more leverage pushing up than pulling out. Due to small sample size of the individuals using the door solution, either solution was considered as a successful innovation. To prevent marmots from flipping the apparatus, each box was secured to a 60.7 × 50.8 cm plywood platform. Both the wooden frame and plywood were sealed with two coats of polyurethane to prevent water damage and to permit cleaning (with concentrated acetic acid) between deployments to different colonies.

Puzzle boxes were deployed from 3 June to 1 July 2018. Boxes were set out at eight colonies with multiple boxes placed at social groups within colonies depending on group size and distribution of individuals. Each box was set out for a total of 2 weeks at each colony. Weeks were separated into two rotations: a down-valley rotation where the boxes were set out at four lower-elevation colonies: Gothic Townsite, River Annex, River Mound/Bench, Avalanche and an up-valley rotation where boxes were set out at four higher-elevation colonies: Marmot Meadow, Picnic, Boulder and North Picnic. Gothic Townsite had three puzzle boxes set at three distinct social groups that do not interact or overlap in physical space. River Mound and Bench had two puzzle boxes due to physical distance of the two burrows (200 m) that the individuals of the colony moved between. Picnic had two puzzle boxes due to group size (33 individuals). Marmot Meadow previously had two distinct non-interacting social sub-groups and were given two puzzle boxes. However, during the 2018 season, the individuals had significant social overlap and were considered as one social group for this experiment. Boulder, North Picnic, River Annex and Avalanche all had one puzzle box due to low group size and centralized location. Boulder and River Annex did not have enough observations and were dropped from subsequent analysis. The lack of movement of individuals between colonies precluded any potential transfer of knowledge between colonies. Puzzle boxes were placed within 1 m of an active marmot burrow. Marmots tend to be philopatric to their burrows and an active burrow was identified if observers had seen activity there over the past three days.

Each puzzle box was baited with half a cup of Omalene horse feed (Purina® Omolene 100, Purina Mills, LLC, St. Louis, MO, USA), which is a desirable food source also used to bait traps (Fuong et al. 2015). The boxes were all set up before 07:00 h and were freely accessible to the marmots throughout the morning. Individuals started a trial when they stepped with at least one paw onto the plywood and were considered 'interacting' with the box from when they first made physical contact with the box with any part of their body until they no longer had physical contact with the plywood or box for over 5 s, when the trial was considered over. Individuals engaged in 1 to 48 trials a day with an average of 7.5 daily trials and spent 5 s to 896 s at the box with an average visit lasting 80.9 s (standard error ± 3.75). Two Browning Strike Force HD or Browning Spec Ops FHD cameras were placed approximately 2.5 m from the box and aimed at opposite corners of the platform to capture activity from different perspectives. Cameras were movement activated and set to record 2-min videos with a 5-s recovery time.

Measures

Social measures

We used all occurrence behavior sampling to quantify social interactions recorded over the summer season to calculate two separate social networks for each colony from all affiliative or agonistic interactions between yearlings and adults (ethogram listed in Table 1 in Online Resource 1). All networks took into account direction of the interaction (initiator and recipient) and weight of the interaction (number of times the pair interacted). From these networks, we calculated nine social measures (in/out degree, in/out strength, in/out closeness, local clustering, betweenness centrality and eigenvector centrality), which characterize an individuals' position in their social network (specific definitions are listed in Table 1). All calculations were made with the igraph package (Csárdi and Nepusz 2006) in R v. 3.6.1 (R Core Team 2019) and RStudio (RStudio Team 2020).

PCA

To account for correlation between social measures, we used principal component analysis to reduce these traits into three principal components (eigenvalues > 1.0) each for the affiliative and agonistic networks. Principal component analysis (PCA) was conducted with the psych package in R (Revelle 2018).

Principal component loadings are summarized in Tables 2 and 3. We interpreted the first affiliative component as describing *friendliness*; indegree, outdegree, instrength, outstrength and eigenvector centrality loaded heavily on it. Friendly individuals have many strong affiliative relationships. We interpreted the second affiliative component as *isolation*; negative betweenness loaded heavily on it. Isolated individuals did not link the group together. Since this variable was negative in the loadings, it indicates that an interpretation of high isolation indicates low connecting of disparate subgroups. We interpreted the third component as *initiated closeness*; outcloseness loaded heavily on it. These individuals initiated

Table 1 Social network attributes and their definitions

Attribute	Summary
Degree (In/Out)	Number of individuals with whom a focal individual interacted (Wasserman and Faust 1994)
Strength (In/Out)	Total number of interactions involving a focal individual (Barrat et al. 2004)
Closeness (In/Out)	Reciprocal of sum of shortest path lengths between focal and other individuals (Wasserman and Faust 1994; Wey et al. 2008; Fuong et al. 2015)
Betweenness	Number of shortest paths between pairs of individuals that pass through a focal individual's network (Wasserman and Faust 1994; Wey et al. 2008)
Eigenvector centrality	A measure of how well one's direct associates are connected with others (Bonacich 2007; Fuong et al. 2015)
Local Clustering	Fraction of ties to other individuals that a node has over all possible ties a node could form (Opsahl 2013; Watts and Strogatz 1998)

Out indicates interactions initiated by the focal individual and In indicates interactions received by the focal individual. All attributes were extracted from a weighted network, which accounts for the rate of interactions

Table 2 Principal component scores from principal component analysis of affiliative social network measures

	Friendliness	Isolation	Initiated closeness
Indegree	**0.94**	− 0.18	− 0.07
Outdegree	**0.93**	− 0.11	− 0.03
Betweenness	0.38	− **0.78**	0.19
Local clustering	-0.27	0.44	0.53
Outstrength	**0.75**	0.55	− 0.05
Instrength	**0.76**	0.55	− 0.01
Outcloseness	0.03	0	**0.88**
Incloseness	0.33	− 0.46	0.15
Eigenvector centrality	**0.90**	0.01	0.14

Bolded values indicate high loading values included in the component

Table 3 Principal component scores from principal component analysis of agonistic social network measures

	Aggression	Received Aggression	Initiated aggression frequency
Indegree	0.69	**0.64**	− 0.11
Outdegree	**0.88**	− 0.31	0.19
Betweenness	**0.74**	− 0.37	− 0.34
Local clustering	− 0.49	0.18	0.14
Outstrength	0.40	− 0.24	**0.85**
Instrength	0.21	**0.67**	0.06
Outcloseness	**0.78**	− 0.24	− 0.43
Incloseness	**0.70**	0.45	0.06
Eigenvector centrality	**0.76**	0.03	0.23

Bolded values indicate high loading values included in the component

interactions directly with a large portion of other individuals in their network. We interpreted the first agonistic component as *Aggression*; outdegree, betweenness, eigenvector centrality, incloseness, outcloseness loaded heavily on it. Individuals who scored high in this category initiated aggression against a large proportion of others in their network. We interpreted the second agonistic component as *received aggression*; indegree and instrength loaded heavily on it. Individuals who scored high in this category received higher amounts of aggression from others. We interpreted the third agonistic component as *initiated aggression frequency*; outstrength loaded heavily on it. These individuals frequently initiated aggressive interactions towards others.

Dominance rank

To account for potential effects of dominance on innovation success, we used the Clutton-Brock index of social dominance (CBI, Clutton-brock et al. 1979) to calculate relative rank. We used CBI because it excludes rate of interaction from calculations, which is better suited to species with low-frequency interactions like marmots (Bang et al. 2010). The CBI was calculated from a ratio of wins and losses during agonistic events for each individual. The equation for CBI is $(B+b+1)/(L+1+1)$, where B is the total number of individuals 'beaten' who previously lost an interaction to the focal individual, b is the number of individuals who those individuals who were 'beaten' have won against, L is the number of individual 'winners' who have won an interaction with the focal individual, and l is the number of individuals to whom 'winners' have lost (Blumstein et al. 2016).

Relative rank was calculated to account for different numbers of individuals in a hierarchy, here defined as a colony. Each rank was standardized with respect to the total number of individuals present in the group (Huang et al. 2011). CBI values were ordered from lowest to highest to calculate an absolute rank value and then divided by the total number of individuals in the network to calculate relative rank. For each colony, the lowest ranked individual had a relative rank of zero and the highest ranked individual had a relative rank of one.

Behavioral traits

We extracted innovation success and four behavioral traits (persistence, behavioral selectivity, behavioral diversity and neophobia) from video recordings of the marmots at the puzzle box using JWatcher 1.0 (Blumstein and Daniel 2007). After the start of each trial (when a marmot first physically contacted the plywood platform), we recorded the onset of all behaviors an individual engaged in (full ethogram in Table 2 in Online Resource 1) until the end of the trial when the marmot was no longer in physical contact with the plywood platform for longer than 5 s. Behaviors were separated based on which section of the puzzle box the individual touched (door, lid, other part of box) and how they interacted with it (nose, paw, bite, other).

Successful marmots manipulated either one of the two solutions, the door or the lid, to enter the box and thus obtained the food reward (which was confirmed by seeing them chew). All other marmots who initiated trials but did not open the box were considered not successful, even if they obtained the food reward through scrounging. We formally studied scrounging in marmots in a companion paper, although this analysis was conducted on a dataset from 2019 (Evans et al. 2021). Trials in which marmots engaged in no other behaviors than chewing on the plywood for extended periods of time were also removed from the analysis. Only one of the two puzzle box cameras was scored and included in the analysis to prevent repeated observations. Scorers were trained to have repeatable ≥ 0.95 interobserver correlation on test videos before collecting data.

We quantified four behavioral traits commonly measured in relation to innovation success: persistence, behavioral selectivity, behavioral diversity and neophobia. We quantified persistence as the proportion of time in sight that the focal marmot spent interacting with the box during a trial (hereafter, proportion of time). Behavioral selectivity was calculated as the sum of the proportion of time in sight devoted to effective behaviors, defined as actions directed at the door or the lid of the box. For persistence and behavioral selectivity, we excluded all trials during which marmots were on the plywood but did not interact with the puzzle box in order to avoid inflating the dataset with zeros for non-interacting marmots. To account for different trial lengths and number of observations of each behavior per trial, we calculated behavioral diversity with a Shannon index $H = -\sum_{i=1}^{R} (p_i \bullet \log p_i)$ (Pielou 1975), for each individual across each trial. Here, $p_i =$ the proportion of time spent enacting behaviors, such as manipulating the door with their mouth or manipulating the lid with their paw (full ethogram defined in Table 2 Online Resource 1), out of the total time spent in sight on the plywood. The behaviors 'on' and 'off' plywood were excluded from analysis because these behaviors marked the start or end of the trial. To assess an individual's degree of neophobia, we measured the latency to touch the box from stepping onto the platform for the first trial of each day an individual interacted with the box. To account for potential habituation to the box over each day, neophobia was measured only on the first trial of each day that a marmot interacted with the puzzle box. Neophobia could not be calculated for marmots that touched the plywood but did not touch the box and they were removed for these days in the dataset. The neophobia dataset were smaller than those of the other behavioral traits as it was measured a different level (day).

Data analysis

Traits associated with problem-solving success

To test whether social measures or a specific behavioral trait was associated with innovation success (Fig. 1a), we created a series of generalized linear mixed models for behavioral traits and generalized linear models for social measures. All models had a binary measure of problem-solving (success or failure) as the dependent variable. Eleven total models were fitted on six different datasets due to data being measured at different level and are outlined below. The six datasets were behavioral diversity ($N = 547$ observations on 34 individuals), behavioral selectivity and persistence ($N = 365$ observations on 33 individuals), neophobia ($N = 155$ observations on 35 individuals), affiliative attributes ($N = 38$ observations on 38 individuals), agonistic attributes ($N = 26$ observations on 26 individuals) and relative rank ($N = 32$ observations on 32 individuals). Dominance and both social network attributes were measured as a once yearly value and tested against a yearly measure of problem-solving success (individual solved the puzzle at least once over the season = 1, individual did not solve the puzzle over the season = 0). These three variables created three separate datasets due to sample size differences between them. Neophobia was measured for the first trial of each day that an individual interacted with the box and so it was tested against a daily measure of problem-solving success (individual solved the puzzle at least once during that day = 1, individual did not solve the puzzle that day = 0). Behavioral diversity, behavioral selectivity and persistence were measured per trial and were tested against trial-level problem-solving success (individual solved the puzzle during that trial = 1, individual did not solve the puzzle during that trial = 0). However, they were separated into two separate datasets because sample size differences due to the individuals dropped from persistence and behavioral selectivity. These separate datasets were created to avoid statistical issues associated with multiple levels in statistical models (Preacher et al. 2010) and small sample sizes.

Four generalized linear mixed effects models were fitted to test the association of each behavioral trait with problem-solving success. Each model had one fixed effect (behavioral diversity, behavioral selectivity, persistence and neophobia) and individual identity as a random effect to account for repeated measures in each of the behavioral traits. Six generalized linear models were fitted to test the association of social measures and problem-solving success. Three models were fitted with one fixed effect of affiliative PCA (Friendliness, Isolation, Initiated Closeness) and three other models had one fixed effect of agonistic PCA (Aggression, Received Aggression, Initiated Aggression Frequency). One generalized linear model tested the correlation of dominance rank and problem-solving success with a fixed effect of relative rank.

All other model variables (behavioral traits, dominance rank) were centered by subtracting column means and scaled by dividing the centered columns by their standard deviations using the scale function in R to ensure comparability of effect sizes (R Core Team 2019). To account for the binomial nature of success, models had a binomial distribution with link = logit function and to promote convergence, we used the optimizer bobyqa on all models that were unable to converge (Bates et al. 2015b). All models were fitted in the lme4 package (Bates et al. 2015a) in *R* and *p* values (significance level ≤ 0.05) were extracted with the lmerTest package (Kuznetsova et al. 2017).

Evaluation of structural equation models

To test whether social structure acted directly or indirectly through behavioral traits to affect problem-solving success, we used confirmatory path analysis using the directed separation (d-sep) method (Shipley 2000). Structural equation models use path diagrams to incorporate multiple hypothesized causal relationships between variables, which can appear as both predictor and response variables, into a single causal network (Lefcheck 2016). A piecewise approach translates the path diagram into a series of linear equations that can be individually evaluated in a stepwise manner. Directed separation tests are used to determine goodness-of-fit and whether variables are conditionally independent, meaning there are no missing relationships between unconnected variables in the hypothesized model (Shipley 2000). This method allows for more flexibility in fitting non-normal data by incorporating multiple modeling methods, such as the inclusion of random effects (Lefcheck 2016) and binomial dependent variables.

We created twenty-four path models (Fig. 1b), one for each combination of the six social measures and the four behavioral traits. Relative rank was included as a covariate in each model to account for the potential effects of social dominance. Each structural equation model (SEM) contained two models. The first linear model tested was a linear mixed effects model of the relationship between social measures and behavioral trait, which included relative rank as a fixed effect to account for potential dominance effects and a random effect of individual identity (nlme, Pinheiro 2019). The second linear model was a generalized logistic mixed effects model of the relationship between behavioral trait and problem-solving success with a random effect of individual identity (lme4, (Bates et al. 2015a).

Each model was evaluated with the d-sep method to test for missing causal links. This was measured by Fischer's *C*, a combination of all *p*-values for each independence claim, compared with a X^2 distribution with $2*k$ degrees of freedom. The proposed causal pathway is supported when there is low conditional independence. This occurs when C could have happened by chance and where X^2 is greater than 0.05 (Lefcheck 2016).

Problem-solving success was modeled with a binomial distribution with link = logit function and the optimizer bobyqa was included to promote convergence (Bates et al. 2015b). All variables were scaled to standardize them and thus their magnitudes are directly comparable. All tests were run in the piecewiseSEM R package (Lefcheck 2016), which allows each path to be modelled separately using appropriate methods for the variables involved in that relationship.

Analyses were again conducted on six different datasets. Affiliative behavioral selectivity/persistence ($N = 282$ observations on 27 individuals), affiliative behavioral diversity ($N = 404$ observations on 28 individuals), affiliative neophobia ($N = 102$ observations on 27 individuals), agonistic behavioral selectivity/persistence ($N = 265$ observations on 21 individuals), agonistic behavioral diversity ($N = 377$ observations on 22 individuals) and agonistic neophobia ($N = 88$ observations on 22 individuals). Given the number of analyses (even though they were conducted on multiple data sets), we are most confident in results that are highly significant (i.e., $p < 0.001$). We considered strong effects to be those with $p < 0.05$ and weak effects to be those with $0.05 < p < 0.08$.

Results

Thirty-nine unique individuals interacted with the puzzle box. This included 19 adults and 20 yearlings, of which 24 were females and 15 were males. Seven individuals (18%) successfully solved the puzzle box, four of which only ever used the lid and the other three individuals used both the lid and the door. Out of 47 successful trials, the lid was used 36 times (77%) and the door was used 9 times (19%), with 8 door uses being a marmot entering the box through the lid and exiting through the door and returning to eat through the door. Datasets on which statistics were calculated consisted of smaller groupings of these individuals based on limitations of behavioral or social data.

Table 4 GLM results of direct models of social measures and innovation success and GLMM results of direct models of behavioral traits on innovation success

	Effect size	Standard error	*p* value
Behavioral traits			
Persistence	0.147	0.244	0.545
Behavioral diversity	**1.06**	**0.224**	**< 0.001****
Behavioral selectivity	0.290	0.231	0.210
Neophobia	− 0.011	0.630	0.986
Affiliative measures			
Friendliness	− 0.523	0.478	0.273
Isolation	− 0.214	0.386	0.580
Initiated closeness	− 0.285	0.442	0.519
Agonistic measures			
Aggression	0.002	0.504	0.997
Received aggression	**− 1.29**	**0.730**	**0.078***
Initiated aggression Frequency	0.479	0.425	0.260
Relative rank	0.295	0.472	0.532

*Indicates weak support (p = 0.05–0.08), ** indicates strong support ($p < 0.05$)

Bold values indicate significance

Behavioral traits associated with innovation success

We found a positive relationship between behavioral diversity (estimate(SE) = 1.06(0.224), $p < 0.001$) and innovation success. Innovation success was not associated with behavioral selectivity (estimate(SE) = 0.290(0.231), $p = 0.210$), persistence (estimate(SE) = 0.147(0.244), $p = 0.545$) or neophobia (estimate(SE) = − 0.011(0.630), p = 0.986). Received aggression had a negative, but weakly supported, relationship with innovation success (estimate(SE) = − 1.29(0.730), $p = 0.078$).

Neither affiliative social measures, nor relative rank, was correlated with innovation success (full results in Table 4).

Relationships between affiliative social measures and innovation success

After controlling for variation explained by relative rank, there was one path that was weakly supported. Individuals with low initiated closeness were more behaviorally diverse (estimate(SE) = − 0.196(0.097), $p = 0.054$) and more successful at solving the problem (Fig. 3a). Full results are presented in Table 5.

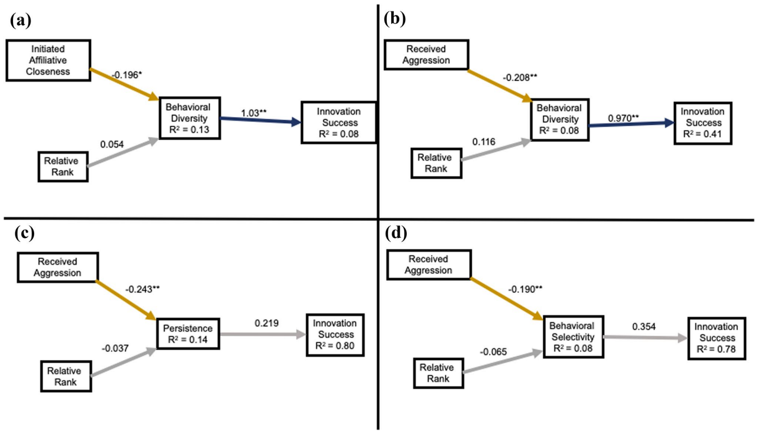

Fig. 3 SEM results. Path diagrams that included strongly or weakly supported effects of different social measures on behavioral traits and problem-solving success. **a** Affiliative initiated closeness and behavioral diversity, **b** received aggression and behavioral diversity, **c** received aggression and persistence, **d** received aggression and behavioral selectivity. Standardized path coefficients are interpreted in terms of standard deviation. Positive effects (+) are shown in dark blue. Negative effects (−) are shown in dark yellow. ** indicates the effect was strongly supported ($p < 0.05$), * indicates the effect was weakly supported ($p = 0.05$–0.08), no support ($p > 0.08$) are shown in grey. Conditional R^2 values are reported for each path

Table 5 Statistical output from path analysis of affiliative measures and behavioral traits

	Fischer's C	*p*	Estimate (PCA → Behavior)	*p*	Estimate (Behavior→ Success)	*p*
Persistence						
Friendliness	0.347	0.987	0.032	0.813	0.204	0.451
Isolation	1.01	0.909	− 0.092	0.370	0.204	0.451
Initiated closeness	1.66	0.798	− 0.042	0.730	0.204	0.451
Behavioral diversity						
Friendliness	0.285	0.991	0.029	0.800	**1.03**	**< 0.001****
Isolation	1.78	0.777	− 0.096	0.280	**1.03**	**< 0.001****
Initiated Closeness	1.52	0.823	**− 0.196**	**0.054***	**1.03**	**< 0.001****
Behavioral selectivity						
Friendliness	0.361	0.986	0.042	0.702	0.327	0.216
Isolation	1.01	0.908	− 0.117	0.153	0.327	0.216
Initiated closeness	1.66	0.799	− 0.144	0.127	0.327	0.216
Neophobia						
Friendliness	1.38	0.848	− 0.196	0.136	− 41.32	0.151
Isolation	1.42	0.84	− 0.037	0.723	− 41.32	0.151
Initiated closeness	0.977	0.813	0.078	0.586	− 41.32	0.151

*Indicates weak support ($p = 0.05$–0.08), ** indicates strong support ($p < 0.05$)

Significant Fischer's *C* value indicates that the hypothesized paths are inconsistent with the data and that the relationships could have occurred by chance

Bolded values are significant

Relationships between agonistic social measures and innovation success

Three models, which tested the causal effect of initiated aggression frequency on behavioral diversity, persistence and behavioral selectivity, had a high Fisher's *C* ($p < 0.05$, Table S4), indicating that the proposed causal path was not supported by the data.

After controlling for variation explained by relative rank, only a few paths were strongly supported. Individuals who received fewer aggressive interactions from their neighbors were more behaviorally diverse (estimate(SE) = − 0.208(0.071), $p = 0.009$) and more successful problem-solvers (Fig. 3b). Individuals who received fewer aggressive interactions were more persistent (estimate(SE) = − 0.243 (0.094), $p = 0.018$, Fig. 3c) and more behaviorally selective (estimate(SE) = -0.190(0.081), p = 0.031, Fig. 3d). However, neither of these paths influenced problem-solving success. Full results are presented in Table 6.

Discussion and conclusion

Taken together, we examined whether the propensity to solve a novel problem, a proxy for innovation, was driven by an individuals' behavioral traits, social measures, or dominance rank. We first examined the associations between our 11 variables and problem-solving success and then examined the causal direct and indirect effects of social structure (social measures, controlling for dominance rank) on behavioral traits and problem-solving success. From our correlative results, we found that individuals who are more behaviorally diverse were associated with more successful puzzle box solvers, while those who received more aggression were associated with less successful solvers. We additionally found that social structure affects which behavioral trait an individual uses and thus, indirectly affects problem-solving success. Individuals who initiated affiliative interactions with a greater proportion of their network were less behaviorally diverse, conversely suggesting that less friendly individuals are more successful problem-solvers.

Individuals who received more aggression were not only worse at problem-solving, but they also behaved differently. These individuals employed a less diverse set of behaviors, were less behaviorally selective and less persistent when exploring the box. Although problem-solving performance was only affected by decreased behavioral diversity, the effect of aggression on the other strategies indicates that there are multiple, indirect factors that influence perceived problem-solving ability. Recipients of aggression may be poor problem-solvers because they were prevented, physically or by stress, from engaging in the behavioral traits necessary to solve the problem. We would expect that

Table 6 Statistical output from path analysis of agonistic measures and behavioral traits

	Fischer's *C*	*p*	Estimate (PCA → Behavior)	*p*	Estimate (Behavior → success)	*p*
Persistence						
Aggression	2.29	0.682	0.050	0.652	0.219	0.421
Received aggression	4.31	0.366	**– 0.243**	**0.018****	0.219	0.421
Initiated aggression frequency	**10.8**	**0.029****	– 0.125	0.177	0.219	0.421
Behavioral diversity						
Aggression	4.69	0.320	0.032	0.743	**0.967**	**< 0.001****
Received aggression	6.55	0.162	**– 0.208**	**0.009****	**0.967**	**< 0.001****
Initiated aggression frequency	**23.0**	**0****	0.027	0.735	**0.967**	**< 0.001****
Behavioral selectivity						
Aggression	2.30	0.682	0.138	0.137	0.354	0.185
Received aggression	4.26	0.372	**– 0.190**	**0.031****	0.354	0.185
Initiated aggression frequency	**13.1**	**0.011****	– 0.090	0.256	0.354	0.185
Neophobia						
Aggression	1.48	0.831	– 0.023	0.835	– 12.9	0.289
Received neighbor aggression	2.43	0.656	0.021	0.843	– 12.9	0.289
Initiated aggression frequency	2.49	0.479	0.065	0.464	– 12.9	0.289

*Indicates weak support ($p = 0.05$–0.08), ** indicates strong support ($p < 0.05$)

Significant Fischer's *C* value indicates that the hypothesized paths are inconsistent with the data and that the relationships could have occurred by chance

Bolded values are significant

individuals who were excluded from the puzzle box by aggression would instead scrounge. However, in another study we found that dominance rank, which is calculated from aggressive interactions, was unrelated to whether an individual was a producer (an individual who obtains food for themselves) or a scrounger (an individual who relies on others to obtain food for them) (Evans et al. 2021). Thus, scrounging is unlikely related to social aggression. Interestingly, in this study, relative rank never directly explained variation in behavioral trait or problem-solving success, suggesting that the aggression referred to here is not related to competitive dominance.

Our correlative results were unsurprising given that both behavioral diversity and aggression are common factors considered when studying problem-solving ability. Behavioral diversity is consistently associated with problem-solving success in a number of species (Benson-Amram et al. 2013; Griffin et al. 2014; Daniels et al. 2019) and may be particularly important for generalist species, who are more likely to try different behaviors when searching for or exploiting novel resources (Benson-Amram et al. 2013). Marmots are generalist herbivores primarily feeding on surface level forbs and grasses and thus, they do not typically employ a wide range of foraging-related behaviors (Carey 1985). However, previous studies have found an association between generalist diets and novel object exploration (Bergman and Kitchen 2009; Tebbich et al. 2009), suggesting that for species that have a varied diet, it is advantageous to be more exploratory with potential novel food sources.

Our results on aggression are predicted by the social inhibition hypothesis, which states that problem-solving ability is inhibited in poor competitors because of their preoccupation with fear and risk avoidance in the presence of others (Griffin et al. 2013; Keynan et al. 2016). In Indian mynahs (*Acridotheres tristis*), individuals who were exposed to a novel foraging task in the presence of conspecifics were less likely to solve the task and, if they did, took longer to do so. The influence of conspecifics was context dependent where individuals in "high risk" situations (novel object nearby) were less likely to attempt the task when surrounded by conspecifics compared to a "low risk" situation (no object) (Griffin et al. 2013). In our population, less successful problem-solvers may be more sensitive to "risky" situations, but rather than this risk stemming from fear of a novel object, it comes from fear of receiving aggression from others. Aggression is known to be an important factor structuring marmot social groups (Blumstein et al. 2009; Wey and Blumstein 2010, 2012). While marmots will often share overlapping foraging territories with kin, mothers will exclude others from foraging areas; the propensity to share is shaped by individual behavior, age and reproductive status (Frase and Armitage 1984). Thus, aggressive marmots likely monopolized a desired foraging resource (the bait in the box), leading less aggressive marmots to forage on more easily accessible resources (freely available grass and forbs) to avoid aggression and stressful competition.

Some of our results were unexpected and contrary to findings in other species. Behavioral selectivity (i.e., employing only those behaviors that will be successful) is typically associated with problem-solving success (Benson-Amram and Holekamp 2012; Daniels et al. 2019) and indicates that animals learned effective strategies (Chow et al. 2016). We do not address learning here (exploration of learning in this system in Williams et al. in prep). However, behavioral selectivity measured as a proportion of time may yield different results than those in Chow et al. where it was measured as a proportion of behaviors because efficient behaviors may be inherently less time-consuming.

Interestingly, there was no significant effect of neophobia on problem-solving in any model, despite it typically being an important predictor of success in other species (MacDougall-Shackleton et al. 2011; Benson-Amram and Holekamp 2012; Daniels et al. 2019). Our population may have been less neophobic because they were habituated to man-made objects in their environment; they are exposed throughout their lives to livetraps used to trap them every other week. Alternatively, we may have measured neophobia in a way that did not capture the full trait variation within the population. We may have artificially excluded the more neophobic individuals of the population by only measuring those individuals who approached the box and truncated the approach latencies of other individuals, who could have seen the box upon exiting their burrows and were unafraid of the novel object by the time they stepped onto the plywood.

Our results demonstrate that social interactions can indirectly limit or change how an individual approaches a novel problem. In particular, we found that aggression, but not dominance rank, structures problem-solving and access to a novel food source within yellow-bellied marmot colonies. Thus, different types of social interactions may affect problem-solving in different and complex ways. When studying innovation in wild populations, it is difficult to exclude these numerous physical or social factors that directly or indirectly impact an individuals' interaction with a novel task. However, by not investigating these factors, we leave out important ecological context that frames innovation as a potential cognitive ability with fitness consequences. Structural equation modeling provides a statistical method through which to test these various indirect and direct effects and to model pathways between traits, sources of information, environmental conditions and innovation ability. Future studies of innovation would benefit from applying this approach.

Data and code availability

The Data and R code for this paper are available in Github repository: https://github.com/dmwilliams237/Marmot_SEM_Innovation.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10071-020-01464-2.

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Author contributions Conceptualization, DMW, DTB and CW; methodology DTB and DMW; investigation DMW and CW; formal analysis DTB, DMW and CW; writing-original draft DMW and CW; writing—review & editing DMW, DTB and CW; resources DMW and DTB.

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Compliance with ethical standards

Conflicts of interest The authors declare that they have no conflict of interest.

Ethics approval The marmot study population is free-living and could freely interact with or leave the puzzle box as they desired. None were harmed by interacting with the box. Injuries are very rare during trapping and typically involves scrapes that are treated during handling. Marmots were studied under ARC protocol 2001-191-01 by the University of California Los Angeles Animal Care Committee on 13 May 2002, and renewed annually, as well as annual permits issued by the Colorado Division of Wildlife (TR519) and the Rocky Mountain Biological Laboratory's Animal Care Committee.

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Williams DW, Evans A, Briana B, Blumstein DT. Can a generalist herbivore learn to problem-solve? (in preparation)

Chapter 4: Variable learning and social transmission in a non-extractive foraging herbivore

Abstract

Learning is essential for animals to thrive in novel environments, but obtaining information is costly and requires weighing costs and benefits. Individuals learn information from either individual (e.g., by trial-and-error learning) or social (e.g., by copying others' behaviors) sources and seek different information for different situations. We tested learning in a facultatively social, non-extractive foraging herbivore, yellow-bellied marmots (*Marmota flaviventer*), who experience several negative consequences of living socially that impact, among other things, reproductive success and longevity. We predicted that marmots rely more on individual than social learning. First, we asked whether marmots learned to solve a novel extractive foraging task. Second, we asked whether marmots used social or individual information on the location of the task. Third, we asked whether marmots used social or individual information for the skills employed to solve the task. We found that experienced individuals interacted with the puzzle box less during a trial but did not compensate by using more effective behaviors or take less time to open the box. Additionally, social transmission was low; present in 7 of 17 groups for location, and in 2 of 10 groups for solving skill. Overall, individuals used trial and error rather than more efficient solving. They rarely used social information, but when they did, it was on foraging location not motor skills. While non-extractive herbivores may not rely on social learning for foraging, they may use local enhancement, being drawn to an area or object by the presence of others, rather than transmission of more detailed information. Additionally, social learning may still occur in other contexts such as learning to avoid predators. It is important to study species who do not naturally solve complex problems to understand cognitive evolution.

Introduction

Learning allows animals to navigate complex, often rapidly changing, environments to successfully survive and reproduce (Sol and Lefebvre 2000; Sol et al. 2005; Sih 2013; Greggor and Thornton 2016; Reader et al. 2016). To learn new skills, individuals must first obtain information from their environment but information can be gathered from a variety sources across a range of sensory modalities (Dall et al. 2005; Pritchard et al. 2016; Fischer et al. 2017). Obtaining information can be costly and there is a risk that information will be misleading or inaccurate (Kendal et al. 2005c). Thus, individuals must make decisions on how they gather information to minimize costs, while maximizing the information's relevancy.

An important decision individuals must make when gathering information is from whom to seek information. Information can be gathered individually (e.g., through trial-and-error learning) or through social learning (e.g., by copying the actions of others). While individual learning, also known as asocial learning, can be costly in terms of time, energy and increased predation risk (Giraldeau et al. 2002), the information obtained is more likely to be accurate to the current environment. Conversely, social learning allows individuals to reduce the time and energy required to individually acquire information (Galef and Laland 2005), but by doing so, an individual might receive out-of-date or otherwise not useful information. Individuals may flexibly switch between social and individual learning based on a set of "social learning strategies" (Laland 2004) that may include rules for "when" to copy, such as when individual learning becomes too costly, as well as "who" to copy – such as copying only dominant individuals (Giraldeau et al. 2002; Laland 2004).

Teasing apart individual and social learning can be difficult as they both rely on similar underlying processes (Heyes 2012) and likely overlap in use. For example, learning may rely on socially copying a behavioral template, similar to song-learning birds (Soha 2017), which is then perfected through individual trial and error (Truskanov and Lotem 2017). Network-based diffusion analysis (NBDA) is a technique that estimates likelihood of use of individual or social learning while acknowledging their overlap. Specifically, NBDA estimates whether novel behaviors are transmitted socially or individually by analyzing the order of transmission between individuals after accounting for a group's network structure (Franz and Nunn 2009; Atton et al. 2014; Hasenjager et al. 2020). It assumes that more strongly connected individuals will be more likely to transmit information to one another. NBDA incorporates individual learning into a social learning model thus allowing it to assess the strength of reliance on each learning style rather than strictly defining a learning event as solely individual or social (Hoppitt et al. 2010). Through NBDA, the effects of external factors, such as the impacts of age or sex, on individual and social learning can also be assessed (Hoppitt et al. 2010).

Individuals must also decide which stimuli they will pay attention to when gathering information. For instance, individuals may be drawn to the location of a foraging patch by the social presence of others (*local enhancement*), but they may still use trial-and-error learning to figure out what to eat or how to obtain it (Galef 2015). This strategy may also occur with *stimulus enhancement,* when an individuals' attention is socially drawn to a particular object, or in *emulation*, where an individual socially observes the goal that can be achieved but does not copy the process to achieve that goal (Heyes and Galef Jr. 1996). These processes are often studied under captive or laboratory conditions. While the laboratory allows for cognitive abilities to be reliably tested, telling us what animals *can* do, it does not show us how animals use cognitive or other abilities to solve problems as they would in a natural context (Pritchard et al. 2016).

Despite the desire to study cognition and problem-solving in the wild, external factors such as environmental changes, the inability to rigorously apply controls and a lack of records on individuals' previous experiences make it difficult to do so. One way to overcome the unknown of an individuals' previous experience is to experimentally introduce a novel problem to a wild population to ensure that all individuals are equally naïve to it. A popular method is to introduce a puzzle box, a type of novel extractive foraging task, where a reward is presented inside of an object that can be opened by being manipulated in certain ways. Such a method generates innovative behaviors within the population, which can then be learned by naïve individuals (Griffin and Guez 2014). Puzzle boxes are often used to test cognitive abilities of wild animals (Benson-Amram and Holekamp 2012; Griffin and Guez 2014; Borrego and Gaines 2016; Daniels et al. 2019), as well as social transmission (Aplin et al. 2013) and producer-scrounger dynamics (Evans et al. 2021). Thus, they provide an easy-to-use method to test the decisions individuals make while problem-solving.

Yellow-bellied marmots (*Marmota flaviventer*) are facultatively social ground squirrels that live in matrilineal colonies. Marmots at the Rocky Mountain Biological Laboratory have been continuously studied for almost 60 years and are known to interact with and repeatedly solve novel extractive foraging puzzles (Williams et al. 2021). However, it is not known how and if individuals learn when they problem-solve. Female marmots become less socially connected with others as they age (Wey and Blumstein 2010b) and they suffer a variety of negative consequences of affiliative social relationships, including decreased overwinter survival (Yang et al. 2016), reproductive success (Wey and Blumstein 2012b) and longevity (Blumstein et al.

2018). These negative associations with sociality suggest that marmots may be less inclined to learn from one another or would be less likely to pass information directly to one another. Therefore, we predict that marmots will be more likely to learn individually than socially.

We sought to find out if and how this facultatively social mammal learns and to what sources of information they attend. Specifically, we asked: 1) Do marmots show evidence of learning by becoming more efficient puzzle box solvers over time? 2) If individuals learn the location of the puzzle box, do they use individual or social information? And 3) do individuals use individual or social information to learn the solutions to the puzzle box?

Methods

Study system

We conducted experiments in 2018 and 2019 at the long-term study site of yellow-bellied marmots in and around the Rocky Mountain Biological Laboratory (RMBL), located in Gothic, Colorado, USA. RMBL is a high-altitude field station located in the upper East River valley of the West Elk mountains consisting of alpine meadows and conifer and aspen forests that are covered by snow 7-8 months of the year (Blumstein 2013; Armitage 2014). Individuals were live-trapped using Tomahawk livetraps, and individually marked with numbered ear tags for permanent identification, and had their dorsal pelage dyed for identification by observers from afar (Blumstein et al. 2009a). Observers recorded social interactions with binoculars and 15–45× spotting scopes to watch marmots from distances that did not interfere with normal behavior (Blumstein et al. 2009a). Social interactions were recorded from mid-April, when marmots begin to emerge from hibernation, until mid-September when they begin to hibernate. During this period behavioral observations were conducted on most days, weather permitting, during hours of peak activity (7 –10 h in the morning and 16 – 19 h; Blumstein et al. 2009). Observed social interactions were recorded following a defined ethogram (full ethogram in Supplementary Table 1). Marmots were studied at eight geographically distinct colony sites chosen for their accessibility and data availability (discussed below).

Puzzle box design and deployment

We constructed and deployed eight wood-framed, plexiglass puzzle boxes (30.84 x 30.84 x 30.84 cm, Figure 1). Each box could be solved in two ways: by pushing up on a small plexiglass projection on the lid of the box, or by pulling open a hinged door on one side. Both openings were designed to mimic behaviors already in the marmots' repertoires, but they allowed us to test slightly different applications for each solution (e.g., pulling the door open with mouths or forepaws or pushing the lid up primarily with mouth and nose). Additionally, having two solutions allowed us to examine whether social transmission differed between an easy (lid) and difficult (door) solution. Both solutions were held shut by two 5.08 cm Velcro strips to increase the difficulty and prevent accidental opening. To prevent marmots from flipping the apparatus, each box was secured to a 60.7 x 50.8 cm plywood platform. Both the wooden frame and plywood were sealed with two coats of polyurethane to prevent water damage and to permit cleaning with concentrated acetic acid to remove any smells between deployments to different colonies.

Puzzle boxes were deployed from 3 June to 1 July 2018 and 16 June to 22 July 2019, when marmots were actively foraging but prior to pup emergence, at eight colonies for a total of two weeks at each colony. Colonies differed by elevation across the valley: down-valley (elevation range: 2860 m- 2890 m; colonies: Gothic Townsite, River Annex, River Mound/Bench, Avalanche) and up-valley (elevation range: 2930 m – 2970 m; colonies: Marmot Meadow, Picnic, Boulder and North Picnic). Thus, valley position has different dates of snow melt (Armitage 2014) and distinct effects on life history in this population, particularly for reproduction (Van Vuren and Armitage 1991), survival (Ozgul et al. 2006), body mass (Ozgul et al. 2010) and sociality (Maldonado-Chaparro et al. 2015). Down-valley and up-valley sites are typically trapped in weekly blocks (i.e., one week up-valley colonies are trapped, the next week down-valley colonies are trapped). We set puzzle boxes at either up-valley or down-valley colonies where trapping was not occurring each week to avoid interference with other research activities as well as to control for differences in valley position.

Each colony had one or more social groups, which were determined by physical and social overlap. Gothic Townsite had 3 social groups: Doctors, Red Rock, and Happy Valley, which were physically separated from one another (~400 m) and, except for the dominant Gothic Town male, marmots in different groups did not interact with each other. Marmot Meadow had 2 social groups in 2018: Main Talus and Aspen, which occupied opposite ends of the physical colony space (~80 m) and were largely socially isolated from one another. In 2019, Aspen was excluded because that side of the colony was covered with avalanche debris preventing placement of the puzzle box and obscuring vision of individuals during observations. All other colonies had only one social group. Each social group received one puzzle box with a few exceptions. Picnic had two puzzle boxes in an attempt to prevent overcrowding at any single box due to large colony size (N=15 individuals 2018, 14 individuals in 2019). All Picnic individuals frequently interacted with both puzzle boxes and so data from both locations was combined for analyses. In 2019, River Mound and Bench were expected to be separate social groups due to physical separation (~160 m) and received a box at each social group. While individuals exclusively interacted with one box or the other, they had significant social overlap and so we examined transmission around each box separately but used the same social network for both analyses. In 2018, River Mound was not occupied. Marmots who were unmarked, untagged or otherwise could not be identified were excluded from the study.

Because marmots tend to be philopatric to their burrows, the boxes were set up within ca. 1 m of an active marmot burrow each day (activity was determined by observers recording marmot activity within the previous 3 days). Each puzzle box was baited with half a cup of Omalene horse feed (Purina® Omolene 100, Purina Mills, LLC, St. Louis, MO, USA), a known and preferred food for our population. Boxes were set up before 07:00 h and were freely accessible to the marmots throughout the morning observation session. Two Browning Strike Force HD or Browning Spec Ops FHD cameras (Browning, Morgan, UT, USA) were placed approximately 2.5 m from each box and aimed at opposite corners of the platform to capture activity from different perspectives. Cameras were movement-activated and set to record 2 min videos with a 5 s recovery time.

Quantifying innovation

An innovation was defined as whether a marmot could use either of the two solutions (door or lid) to open the puzzle box. From the video recordings, we defined each approach an individual made to the puzzle box as a trial. A trial began when an individual stepped onto the puzzle box's plywood platform and ended when the individual stepped off the plywood for over 5 s, which was the amount of time the camera took to reset and start again. This allowed us to ensure that we did not miss any behaviors. A trial was successful if the individual opened the puzzle box and obtained the food reward inside; unsuccessful trials were ones in which the individual failed to open the box, did not obtain the food reward or scrounged off of an already opened box. As we wished to study individual variation among successful individuals, only successful trials were included.

We used three measures to test for individual learning in our population (Table 1). The first, ‘latency to open the box’, was a temporal measure of efficiency where time to open the box should decrease with increasing experience (Thornton and Samson 2012; 'work time' in Benson-Amram and Holekamp 2012; Cauchard et al. 2013; 'problem-solving efficiency' in Chow et al. 2016). To obtain this measure, we subtracted the time that the individual first interacted with the box from the time it took to open the box. The second, ‘selective persistence’, also known as ‘behavioral selectivity’, measures efficiency and is defined as the percentage of effective behaviors (i.e., touching the door or lid) used by an individual out of all behaviors used when interacting with the box ('behavioral selectivity' in Chow et al. 2016; Quigley et al. 2021). Selective persistence is predicted to increase with experience as individuals learn which behaviors are most effective for opening the box. The third, ‘non-selective persistence’, measures the rate of interaction with the box and is defined as the total number of contacts with the box divided by the total time spent with the box during a trial ('persistence' in Chow et al. 2016; Quigley et al. 2021). Non-selective persistence is predicted to decrease with increasing successful trials as individuals use fewer behaviors to solve the problem. Trials were ordered and numbered by time of occurrence for each individual. Individuals were assigned sex, age category (adult: 2 years or older, yearling: 1 year old) and categorized as living up-valley or down-valley. All videos were scored using JWatcher 1.0, an event recorder designed to capture the time onset of activities from focal observations (Blumstein and Daniel 2007).

Question 1: Do marmots show evidence of learning?

We analyzed each year (2018 and 2019) separately for two reasons. First, social group structure differs across years. Second, there was substantial variation in snowmelt, rainfall, and therefore food abundance and length of active season across these two years, which might have influenced the motivation to interact with a novel object. Each year we measured the learning latency trends over time for all individuals who were successful at least once. To avoid low sample sizes, we only examined individual learning for overall success rather than separately examining learning for each solution (door versus lid). Only individuals who had successfully solved the box ≥ 3 times for either solution were included in the analysis dataset to ensure that individual variation between trials could be estimated. The Avalanche and River Annex colonies were not included in the statistical analysis because no individuals from those colonies successfully opened the box.

To determine how each individual's learning measures (latency to open the box, selective persistence, and non-selective persistence) varied across successful trials, we fitted a series of increasingly complex mixed effects models which varied by their inclusion of random intercepts, random slopes and fixed effects and are specified below and in Table 1. By fitting different models, we were able to explore different relationships between trial, learning measures and individuals, ultimately allowing us to select a relationship that held the greatest explanatory power. Six of these model series were created, one for each learning measure, each year.

Each model series included four models. The null model, Model 0, evaluated whether there was significant intra-individual variation across all successful trials in the learning measures. This model included the random intercept of individual. For the latency to open the box model series, we additionally calculated the intra-class correlation coefficient (ICC), to determine the intra-individual repeatability of latency (Bell et al. 2009). Model 1 tested whether the addition of explanatory variables improved the fit of the model. Explanatory variables: sex, age category (adult or yearling), and valley position (up-valley or down valley) were added as fixed effects to Model 0. Due to small sample size, only one fixed effect could be included in Model 1 at a time, leading to three versions of Model 1 with one fixed effect each. These different versions were compared with Akaike Information Criterion corrected for small samples (AICc) value and the model version with the lowest AICc was ultimately chosen to be included as Model 1 in that model series. Thus, the analyses for each model series may control for a different fixed effect. Model 2 tested whether an average learning measure for the marmot population changed over repeated trials. To do this, we added an additional fixed effect of successful trial number (where each successful trial was ordered by time that it occurred, e.g., An individual's sixth successful trial is given a 6) to Model 1. Finally, Model 3 tested whether an individuals' learning measures changed across multiple trial by adding successful trial number as a random slope to Model 2. The fits of the four nested models were compared using ANOVA and AICc was used to identify the best fitting model (Zuur et al. 2009).

Due to different data distributions, each learning measure was fitted with a different type of model. Latency to open the box is a continuous variable and was fitted with linear mixed effect models assuming a gaussian distribution. Latency to open the box was log transformed to meet assumptions of normality. Selective and non-selective persistence are rates composed of count occurrence data and were fitted with generalized linear mixed effects models assuming a Poisson distribution (with a log-link function). To model rate data calculated from count data either over time or grouping, the rate can be decomposed into the count data and time or grouping. The count data is included in the model as the dependent variable and the log of the time or grouping is included as a fixed effect offset. For selective persistence this led to number of selective behaviors as the dependent variable and the log of the total number of behaviors performed as a offset fixed effect. For non-selective persistence, the total number of behaviors performed was the dependent variable and log of the total time before success as a fixed effect offset. The fixed effect offset was included in all models in the selective and non-selective model series, including the null model. Model assumptions were evaluated; deviance residuals were approximately normal and q-q plots reasonably straight. For models that would not converge, we used the optimizer function "Nelder-Mead" from the lmerControl parameter (Bates et al. 2015). All generalized linear mixed models were fitted with the packages 'lme4' (Bates et al. 2015) and 'lmerTest' (Kuznetsova et al. 2017) in R v. 3.6.3 (R Core Team 2020). Graphs were created in the package 'ggplot2' (Wickham 2015).

We additionally tested whether there was improvement in performance independent of the mixed models by using a paired t-test to compare the latency to open the box on an individuals' first success and their second success.

Social Transmission and NBDA

We studied social learning during two events. First, we asked whether the order by which marmots first arrived at the puzzle box was influenced by their social relationships. Second, we asked whether the order by which marmots first acquired an innovation skill – opening the lid or door – was influenced by their social relationships.

To test whether these two events occurred via social or individual learning, we used network-based diffusion analysis (NBDA), a method that infers social acquisition of novel behaviors if the order (order of acquisition diffusion analysis: OADA) or time sequence (time of acquisition diffusion analysis: TADA) of acquisition by individuals follows their group's social network structure (Franz and Nunn 2009; Hoppitt et al. 2010; Atton et al. 2014). Despite having time-ordered data available, we chose to use an OADA model because it makes no assumptions regarding baseline learning rates and performs better when baseline learning rates are unpredictable (Hasenjager et al. 2020). There appeared to be different relationships between the three learning measures and the individual as well as different levels of inter-individual variation in learning, we concluded that baseline learning rates were unpredictable. Additionally, a number of factors may have varied between groups, including weather, foraging availability, and individual motivation, which would have contributed to an unpredictable baseline learning rate. In OADA, the social transmission model consists of a pre-determined individual learning factor multiplied by a social transmission factor which predicts the probability of transmission between a naïve and an informed individual from the strength of their social relationship. This social transmission model is compared for best fit with a predicted model of probability of an individual becoming informed solely based on the individual learning factor (Hasenjager et al. 2020). NBDA requires an association matrix of interactions of all individuals in the social group, and the order of their interactions with the puzzle box. For each social group-year and each solution (door or lid), we fitted one set of OADA models comparing the probability of social transmission to individual learning. These analysis were performed with the NBDA package in R v.0.9.5 (Hoppitt et al. 2020).

We used an Akaike information criterion corrected for small sample size (AICc) to determine best fit model between the individual and social models (Burnham and Anderson 2002). Significance for the best fit model was estimated with a likelihood ratio test (Morgan 2008; Hasenjager et al. 2020).

To estimate the order of interaction with the puzzle box, we ranked every individual by the order in which they first exhibited an interaction with the puzzle box (i.e., first approach to the box and first successful use of the door/lid solution) in their social group. Then, we created an association network for each social group each year. To do so, we used all social interactions recorded over the 2018 and 2019 seasons (full ethogram described in Supplementary Table 3.1), except for any interactions with pups (individuals born that summer). These interactions were used to create an association matrix, which captures each individual's number of interactions with each other individual in the network. This matrix included both weight (number of times the pair interacted) and direction (separately counted interactions based on initiator and recipient) of the interactions. Association matrices were built with the igraph package (Csardi 2015) in R v.3.6.3 (R Core Team 2020). Due to overfitting constraints, we could only fit OADA models for social groups where ≥ 3 individuals engaged in an interaction with the puzzle box.

Question 2: Do individuals use individual or social information to learn the location of the puzzle box?

We conducted this analysis on data from eight social groups from 2018 (group sizes: 4-16 individuals) and nine social groups in 2019 (group sizes: 3-17 individuals, Supplementary Table 3.2 for model sample sizes). An individual's order of interaction with the puzzle box was determined by their first trial (i.e., first time stepping on the plywood platform) during the experiment that year in that social group. One exception was the Gothic Town male, who in both years interacted with multiple, otherwise isolated, social groups and puzzle boxes. We included him in each social group with his order of interaction puzzle box ranking based on his first approach to the puzzle box located at that social group. We acknowledge that this may reduce our ability to detect social learning by removing a potential transmission link between these social groups.

Question 3: Do individuals use individual or social information to learn the solutions to the puzzle box?

We used NBDA to test social transmission of the two puzzle box solutions: using the lid to open the box or using the door to open the box. No social group in 2018 had ≥ 3 marmots successfully solve the box with either solution so we did not conduct an analysis on data from 2018. In 2019, we tested 10 social groups--6 with the lid solution (Boulder, Gothic Town-Red Rock, River Mound/Bench, Picnic and North Picnic) and 4 with the door solution (Boulder, Gothic Townsite-Happy Valley, Picnic and Marmot Meadow, Supplementary Table 3.2 for model sample sizes).

Results

In 2018, six unique individuals successfully opened the puzzle box more than two times. Four individuals innovated using only the lid solution and two individuals innovated using both solutions. However, marmots overwhelmingly preferred the lid solution. Out of 47 successful trials for individuals who opened the puzzle box more than three times, only the lid was used 40 times and only the door solution was used 5 times.

In 2019, 15 unique individuals successfully opened the box more than two times. Nine individuals innovated using only the lid solution, one innovated using only the door solution and five innovated using both solutions. Marmots overwhelmingly preferred the lid solution. Out of

39 successful trials for individuals who succeeded more than three times, the lid was used 32 times and the door solution was used 5 times. There were two trials where individuals used both the lid and the door solution in the same trial.

Individual Learning

Latency to open the box was a measure of total time spent interacting with the box. In 2018, the null model, Model 0, was the best fit model (Table 3.2). This model measures how much individuals varied in their latency to open the box. It does not include number of trials, which would indicate an whether an individuals' latency to open the box varied depending on how many trials the individual had done, or fixed effect of valley position, which would indicate that an individuals' latency to open the box could be partially explained by environmental conditions experienced by the individual. However, the model was singular, indicating that model variances were close to 0, and ICC could not be calculated due to lack of random effect variance (Table 3.3). There was no difference in an individual's latency to open the box between their first and on their second successful trials (paired t-test (4); t = 0.955, p = 0.394), indicating that .

The best-fit model for latency to open the box in 2019 was Model 1, which included the fixed effect of valley position (Table 3.2). This model measures both how much individuals varied in their latency to open the box and indicates that some of this variation was explained by their position in the valley. Indeed, individuals up valley had significantly longer latencies than individuals down valley (linear mixed effects model; estimate = 0.935, standard error = 0.356, p = 0.025, Table 3.4), indicating that they spent longer interacting with the box before opening it. ICC indicated that latency had a repeatability of 0.26, indicating that individuals were moderately consistent in how long it took them to open the box. There was also a significant increase (paired t-test; mean = 67.8, CI = 11.614 to 123.986) in latency between the first successful latency and the second successful trials (paired t-test (14); t = 2.59, p = 0.021), indicating that

The best-fit model for non-selective persistence in 2018 was Model 2 (Table 3.2), which indicates that some intra-individual variation was explained by their age category and number of trials. Indeed, younger individuals had significantly lower non-selective persistence than adults (generalized linear mixed effects model; estimate = -1.32, standard error = 0.305, p < 0.001) and non-selective persistence significantly decreased over number of trials (generalized linear mixed effects model; estimate = -0.146, standard error = 0.043, p < 0.001, Table 3.5), with individuals decreasing non-selective persistence the more times they interacted with the puzzle box. Model 2 was additionally over-dispersed (β = 7.65). There was a marginal increase in non-selective persistence (paired t-test; mean = 0.066, confidence interval (CI) = -0.0059 to 0.139) between an individual's first and second successful trials (paired t-test (5); t = 2.36, p = 0.065).

The best-fit model for non-selective persistence in 2019 was the random intercept, random slope model, M3 (Table 3.2). This model indicates that some intra-individual variation was explained by both age category and number of trials, but also that the way that non-selective persistence changed over trial was different for each individual. There was a non-significant trend for yearlings to have higher non-selective persistence than adults (generalized linear mixed effects model; estimate = 0.309, SE = 0.168, p = 0.066, Table 3.6), but there was no overall trend in how non-selective persistence changed over trial (estimate = 0.012, SE = 0.085, p = 0.892). This model was also over-dispersed (β = 8.24). There was no difference in non-selective persistence between first successful latency and second successful latency (paired t-test (11); t = -0.326, p = 0.751).

The best-fit model for selective persistence in 2018 was the null model, Model 0 (Table 3.2), which only measured the intra-individual variation in selective persistence. Given that including trial as a fixed effect did not improve the model, suggests that there was no effect of trial on selective persistence (Table 3.7). This model was also over-dispersed ($\beta = 4.52$). Selective persistence marginally decreased (paired t-test; mean = -0.298, CI = -0.665 to 0.067) between an individual's first and second successful trials (paired t-test (5); $t = -2.27$, $p = 0.086$), suggesting that individuals actually used fewer effective behaviors during their second attempt to solve the puzzle box than their first attempt.

The best-fit model for selective persistence in 2019 was also the null model, Model 0 (Table 3.2), again measuring intra-individual variation in selective persistence and indicating that there was no effect of trial on selective persistence (Table 3.8). However, this model was also over dispersed ($\beta = 3.8$). There was no difference in selective persistence between an individual's first successful and the second successful trial (paired t-test (11); $t = -0.792$, $p = 0.445$), suggesting that individuals used the same amount of effective behaviors in their first and second attempts to solve the puzzle box.

Social Learning

Social transmission of location

We tested whether first arrival at the puzzle box was related to social relationships across nine social groups. In 2018, only two colonies, Picnic and Marmot Meadow - Main Talus, out of eight tested showed evidence of social transmission of location (Table 3.9). For Picnic, the social model fit 4.67x better than an individual model ($p = 0.014$) and for Marmot Meadow-Main

Talus, the social model fit 29x better than an individual model, (p = 0.003). In 2019, five out of nine colonies showed evidence of social transmission of location (Table 3.9). For Marmot Meadow-Main Talus, the social model fit 235x better than an individual learning model (p < 0.001). For Picnic, the social model fit 33.1x better than the individual model (p = 0.002). For Gothic Town-Happy Valley, the social model fit 668x better than the individual model (p < 0.001). For Bench, the social model fit 0.59x better than the individual model (p = 0.026). For River, the social model fit 825x better than the individual model (p < 0.001).

Social transmission of solving skill

We tested social transmission in 2019 for ten transmission paths across six colonies; six paths were tested for the spread of the lid solution and four paths were tested for the spread of the door solution. For the lid, Marmot Meadow-Main Talus showed significant evidence of social transmission (p = 0.026, Table 3.10) fitting 2.29x better than an individual learning model. For the door, Gothic Town-Happy Valley colony showed significant evidence of social transmission (p = 0.03, Table 3.10) and the model was 0.423x better than the individual model. All other five colonies showed that individuals likely learned from trial and error rather than copying (Table 3.10).

Discussion

Overall, it appears that marmots are socially drawn to foraging locations by the presence of others but individually solve tasks through trial and error. However, they do not learn to associate certain actions, such as manipulating a door or lid, with solving the task nor do they turn to social learning when seeking to solve a complex problem. We found that for two of our three individual learning measures–latency to open the box and selective persistence–there was no significant change with increased experience. However, in 2018, individuals were less selective on their second trial than their first trials and, in 2019, individuals took longer on their second trial than their first. Both of these trends were opposite to our expectations, supporting the idea that individuals repeatedly used trial and error when attempting to solve the puzzle box. For non-selective persistence, the best fit models for both years included trial but showed opposite trends of rate of interaction with experience. However, trial was only significant in 2018 where there was a significant decrease in non-selective persistence across trials. This suggests that while more experienced individuals do not necessarily become more efficient at solving a puzzle box, they may still become better at using trial and error to solve it. The diversity of results across our three measures highlights the importance of incorporating multiple measures into tests of cognition. Cognitive abilities are often difficult to isolate and identify and similar to the field of animal personality, animal cognition suffers from low repeatability. This is particularly important for common measurements, such as latencies, which may be affected by internal motivational changes such as hunger (Cauchoix et al. 2018). By testing learning in multiple ways, we are better able to understand the subtleties in how individuals are using their cognitive abilities and how context may influence different measurements.

Marmots also appear to use social information when learning, but they may not do so frequently. Foraging location was socially transmitted in 7 out of 17 groups for puzzle box location across both years while, in 2019, transmission of the lid solution only occurred in 1 out of 6 groups and transmission of the door solution occurred in 1 out of 4 groups. Two social groups, Picnic and Marmot Meadow – Main Talus, showed evidence of social transmission of location in both years, while only Marmot Meadow-Main Talus showed evidence of social transmission of both location and motor skills in 2019. This trend of using social information to find food is well-known in rats and other rodents who prefer food eaten by conspecifics (Valsecchi and Galef Jr 1989; Galef Jr and Heyes 1996). In other species, individuals often prefer foraging patches occupied by conspecifics because it may indicate that a patch is profitable or safe from predators (Midford et al. 2000). While this may explain the difference in frequency between social transmission of foraging location and solution transmission, overall marmots did not use social information all that frequently. This may be because animals often turn to social learning when information is difficult to obtain individually ('copy when individual learning is costly' rule, Giraldeau et al. 2002; Laland 2004). However, marmots are also non-extractive herbivores whose primary food source, herbaceous vegetation, is easily accessible and does not require complex manipulation. For marmots, individual learning may never be particularly costly and they may not be primed to use social information the way animals who face more complex foraging problems do. As another example, in primates, folivorous species have smaller brain size, a measure of cognitive ability, than frugivorous species whose food source requires spatial and temporal memory to find (Clutton-Brock and Harvey 1980; DeCasien et al. 2017). This potential connection between diet type and cognitive ability may provide support for the ecological intelligence hypothesis, which claims that ecological complexity drives the need for and evolution of cognitive abilities (Parker and Gibson 1977). However, marmot cognition and diet type would need to be tested against cognitive abilities of other sciurids with a greater number of diet types to determine whether they provided support for this hypothesis.

While our small sample size prevented us from testing such potential life history traits associated with social learning, we did find several factors associated with individual learning.

Age had opposing effects on non-selective persistence across years, where younger individuals had lower interaction rate with the puzzle box (non-selective persistence) in 2018 but had a marginally higher interaction rate in 2019. Younger individuals in other species are often more exploratory and spend a greater amount of time interacting with puzzle boxes (e.g., hyena *(Crocutta crocuta)* (Benson-Amram and Holekamp 2012), callitrichid monkeys *(spp. Callitrichidae)* (Kendal et al. 2005a; Federspiel et al. 2019) perhaps due to lower neophobia in young or greater propensity to play, including with objects (Reader and Laland 2003). Potentially, the opposing effects may have been due to a difference in dataset size as there was a 1.5x increase in participation in the puzzle box experiments in 2019. Alternatively, different environmental conditions between the two years may have driven yearling marmots, over half of whom disperse over the summer, to have higher motivation for the desired food resource (molasses enriched horse food). In 2019, snow cover was sparse until the spring with the majority of the winter's snow arriving in April and May (barr 2021). Due to this unusual pattern of snowfall, marmots emerged from hibernation later than normal and had lower body mass. Motivation particularly in juveniles, is thought to drive innovation across a wide-range of species (review in Griffin and Guez 2014), and is also associated with increased exploration of a puzzle box (Sol et al. 2012). These yearly differences in food motivation may have also explained our result that individuals who lived up-valley in 2019 took longer to open the box. This hypothesis would require more years of data to formally test.

We did find high inter-individual variation in learning measures in response to increased experience with the box, with some individuals getting surprisingly worse at solving the box as time went on (Figures 2, 3). Noise is a common issue in cognitive tests implemented in the wild because both inter and intra-individual variation can be affected by internal states such as hunger and motivation (Boogert et al. 2018). Additionally, cognition tests often have low repeatability due to the difficulty in isolating a single cognitive process during testing (Cauchoix et al. 2018). Thus, more testing would need to be done to determine whether inter-individual cognitive ability was consistent in this species and whether this difference between individuals had an effect on the group.

Overall, we found that marmots use multiple sources of information during foraging, but they are more likely to solve extractive foraging tasks through individual rather than social learning. When they do rarely use social information, they are more likely to pay attention to a foraging location rather than an extractive skill. As non-extractive herbivores, social learning may be an inefficient method of foraging compared to individual learning. However, this does not mean that marmots would not rely on social learning in other contexts such as learning to identify predators. In this case, social learning may not be generalizable between contexts and social information is most attended to in contexts where it is truly beneficial to the individual or where asocial information is difficult to obtain. While many cognition studies focus on species who solve complex tasks, there is a need to study the cognitive abilities of species who are not complex problem solvers to better understand the evolution of cognitive abilities. Furthermore, by using multiple measurements of cognitive abilities, we can better understand how individuals use cognitive abilities when solving problems.

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Figures and Tables

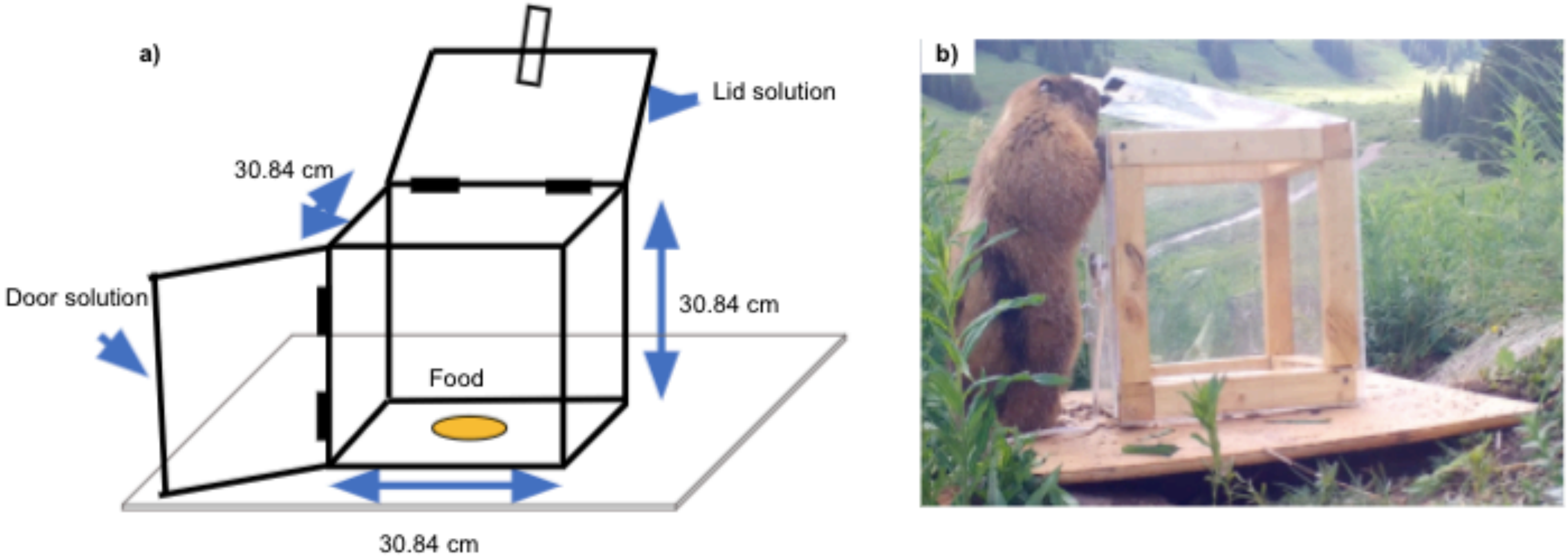

Figure 3.1. Puzzle box design. a) Diagram of puzzle box components. The puzzle box has a wooden frame (30.84 x 30.84 x 30.84 cm) with plexiglass sides. There is a hinged door and a hinged lid with a small plastic protrusion that allow access to the box. The puzzle box is affixed to a plywood base (60.7 x 50.8 cm). b) Photograph of actual puzzle box. Figure modified from Williams et al. 2021.

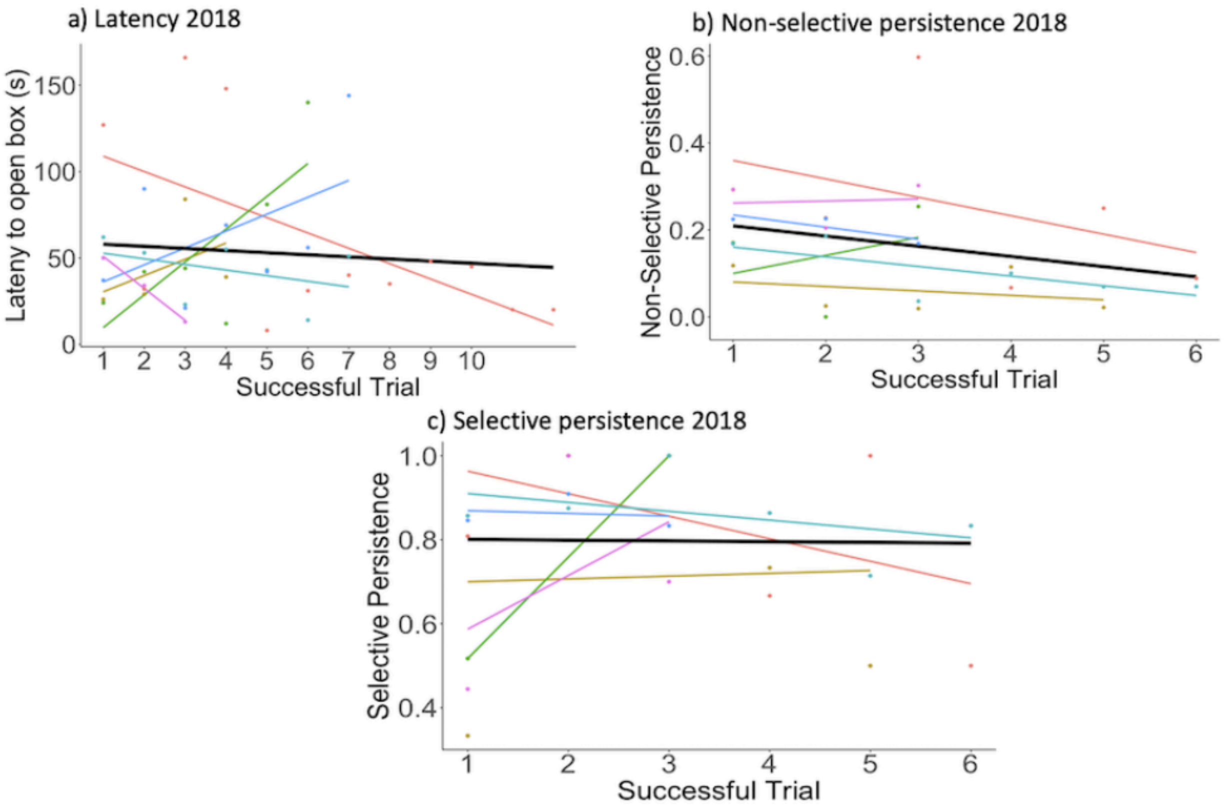

Figure 3.2. **Individual learning latencies** for a) latency to open the box in 2018, b) non-selective persistence in 2018, c) selective persistence in 2018. Trial number represents the number of successful trials the individual engaged in. Only individuals who used the lid solution ≥ 2 times were included. Lines and data points are colored by individual. Black bold line is the population average. Lines projected from a basic linear model of learning measure as dependent variable and successful trial as independent variable.

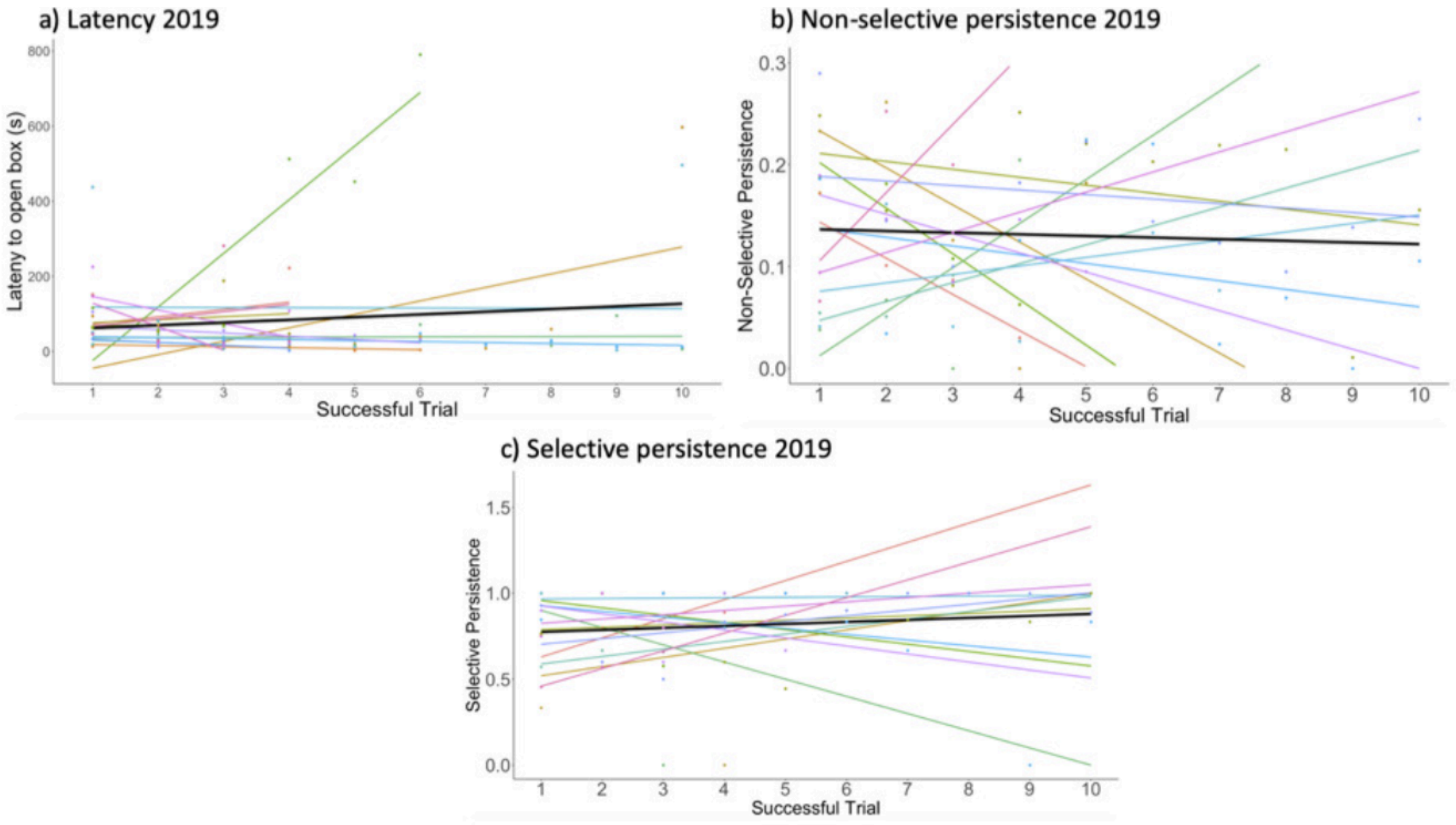

Figure 3.3. **Individual learning latencies** for a) latency to open the box in 2019, b) non-selective persistence in 2019, c) selective persistence in 2019 the first 10 trials per individual. Trial number represents the number of successful trials the individual engaged in. Only individuals who used the lid solution > 2 times were included. Lines and data points are colored by individual. Black bold line is the population average. Lines projected from a basic linear model of learning measure as dependent variable and successful trial as independent variable.

Table 3.1. Summary of definitions and statistical tests used for the three measures of learning.

Learning Measure	**Definition**	**Statistical Test**	**Family**	**Predicted trend over trials**
Latency to open the box	Amount of time individual took to open the box from the time the individual first touched the box during trial (measured in seconds)	Linear mixed effects model	Gaussian	Decrease
Selective persistence	Percentage of effective behaviors (i.e., any interaction with the lid or door) out of all behaviors used by an individual during a trial	Generalized linear mixed effects model with offset of log total # behaviors	Poisson with link=log	Increase
Non-selective persistence	Total number of contacts with the box out of total amount of time spent interacting with box from start of trial	Generalized linear mixed effects model with offset of log total time spent interacting with the box	Poisson with link=log	Decrease

Table 3.2. AICc for linear mixed-effects models compared to study variation in selective persistence (S) and cube-root transformed non-selective persistence (NS) across each dataset. AIC difference > 2 indicates significance and are bolded. For 2018 Latency, valley position and age category had the same AICc score.

Model	AICc					
	2018 Latency	2018 NS	2018 S	2019 Latency	2019 NS	2019 S
M0 - Random intercept	**93.1***	184	**109**	368	771	**353***
M1- Fixed effects, random intercept	95.7 (valley position, age category)	179 (age category)	111 (age category)	**364 (valley position)**	765 (age category)	**354* (sex)**
M2 - Fixed effects + trial, random intercept	102	**170**	114	372	750	355
M3 - Fixed effects + trial, random slope/random intercept	107	176	121	374	**734**	360

* indicates models were not significantly different

Table 3.3. Results of M0, the best fit linear mixed-effects model and null model for 2018 latency to open the box with latency to open the box from first touch as dependent variable and unique individual identity number as random intercept. Bold indicates significance. This model was singular.

Fixed Effects:	Estimates	Standard Error	p -value
Intercept	**3.74**	**0.115**	**<0.001**
Random Effects:		Variance	Std. Dev
UID		0	0
Residual		0.517	0.719

Table 3.4. Results of best fit linear mixed-effects model, M1, for 2019 latency with latency to open the box from touch as dependent variable, fixed effect of valley position (reference level: down valley) and unique individual identity number as random intercept. Bold indicates significance.

Fixed Effects:	Estimates	Standard Error	p -value
Intercept	**3.00**	**0.298**	**<0.001**
Valley Position (Up Valley)	**0.935**	**0.356**	**0.025**
Random Effects:		Variance	Std. Dev
	UID	0.220	0.469
	Residual	1.02	1.01

Table 3.5. Results of best fit linear mixed-effects model, M2, for 2018 non-selective persistence with non-selective persistence as dependent variable, fixed effects of age category (reference level: adult) and successful trial and unique individual identity number as random intercept. Bold indicates significance.

Fixed Effects:	Estimates	Standard Error	p -value
Intercept	**-8.25**	**0.152**	**<0.001**
Age Category (Y)	**-1.32**	**0.305**	**<0.001**
Successful Trial	**-0.146**	**0.043**	**<0.001**
Random Effects:		Variance	Std. Dev
	UID	0.045	0.212

Table 3.6. Results of best fit linear mixed-effects model, M3, for 2019 non-selective persistence with non-selective persistence as dependent variable and age category (reference: adult) and successful trials as fixed effect and unique individual identity number as random intercept with successful trials as random slope. Bold indicates significance.

Fixed Effects:	Estimates	Standard Error	p -value
Intercept	**-9.22**	**0.243**	**<0.001*****
Age Category (Y)	0.309	0.168	0.066
Success trial	0.012	0.085	0.892
Random Effects:		Variance	Std. Dev
	UID	0.528	0.727
	Success trial	0.071	0.266

Table 3.7. Results of best fit linear mixed-effects model, M0, for 2018 selective persistence with selective persistence as dependent variable and unique individual identity number as random intercept. Bold indicates significance. This model was singular.

Fixed Effects:	Estimates	Standard Error	p -value
Intercept	**-0.313**	**0.065**	**<0.001**
Random Effects:		Variance	Std. Dev
UID		0	0

Table 3.8. Results of best fit linear mixed-effects model, M0, for 2019 selective persistence with selective persistence as dependent variable and unique individual identity number as random intercept. Bold indicates significance.

Fixed Effects:	Estimates	Standard Error	p -value
Intercept	**-0.363**	**0.042**	**<0.001*****
Random Effects:		Variance	Std. Dev
	UID	0	0

Table 3.9. Likelihood ratio test (LRT), the relative support that each model is the best K-L model and p-value for OADA results on social transmission of location recruitment in 2018 and 2019. Bold indicates models where social transmission was a significantly better fit than models of individual learning.

Year	**Group**	**LRT**	**Relative Support**	**p**
2018	Avalanche	1.96	0.133	0.161
	Bench	0	0.050	1
	Gothic Town-Doctors	0.315	0.261	0.575
	Gothic Town-Happy Valley	0	0.189	1
	Gothic Town-Red Rock	0.442	0.236	0.506
	Marmot Meadow-Aspen	1.75	0.120	0.185
	Marmot Meadow-Main Talus	**9.31**	**29.08**	**0.003**
	Picnic	**6.08**	**4.67**	**0.014**
2019	**Bench**	**4.95**	**0.59**	**0.026**
	Boulder	0	0.05	1
	Gothic Town-Red Rock	2.52	0.666	0.112
	Gothic Town-Happy Valley	**15.45**	**668**	**<0.001**
	Marmot Meadow-Main Talus	**13.42**	**235**	**<0.001**
	North Picnic	0.003	0.189	0.957
	Picnic	**9.66**	**33.1**	**0.002**

River Mound	**16.0**	**825**	**<0.001**
River Annex	0.245	0.279	0.621

Table 3.10. Social transmission of puzzle box solutions in 2019. Likelihood ratio test (LRT), the relative support that each model is the best K-L model and p-value for OADA results on seven social groups. Bold indicates models where social transmission was a significantly better fit than models of individual learning.

Solution type	**Group**	**LRT**	**Relative Support**	**p**
Lid	Gothic Town-Red Rock	1.42	0.101	0.234
	Marmot Meadow	**4.99**	**2.29**	**0.026**
	Picnic	0.234	0.21	0.628
	North Picnic	0.121	0	0.728
	River Mound	0.765	0.073	0.382
	Boulder	0.811	0	0.368
Door	**Gothic Town-Happy Valley**	**4.28**	**0.423**	**0.039**
	Marmot Meadow	1.53	0	0.215
	Picnic	0	0.050	1
	Boulder	0.811	0	0.368

APPENDICES

A.1 Chapter 2: Supplement

Supplementary Table A.1.1. Ethogram of social behaviors recorded during marmot observation. Each behavior description is written with a focus on the initiator individual. Adapted from Wey and Blumstein 2010.

Relationship Type	**Category**	**Behavior**	**Behavior Description**
Aggression			
	Fight	Interactions happen quickly and marmots separate quickly afterwards. Interactions more likely to be accompanied by vocalizations (squeaks, yelps, growls, etc.). There are eight types of fight behavior.	
		Bite	Initiator bites receiver in an aggressive manner
		Box	Initiator stands on hind legs, using paws to strike opponent in an aggressive manner
		Chase	Initiator chases receiver in an aggressive manner
		Grab/slap/push	Initiator grabs, slaps, or pushes receiver in an aggressive manner
		Mouth spar	When both initiator and receiver lunge at each other with open mouths in an aggressive manner
		Pounce	Initiator pounces on receiver in an aggressive manner
		Snap/snarl/ hiss	Initiator vocalizes in an aggressive way towards a receiver
		Wrestle	Initiator and receiver wrestle with each other in an aggressive manner
Displacement			

		Simple Displacement	There is contact between two marmots and one ends up changing locations
		Proximity Displacement	Initiator marmot approaches other within 1 meter and other individual moves.
Affiliative	*Play*	Unlike aggression, play is 'bouncier' and individuals change roles repeatedly, regularly changing behaviors. Play can get interrupted where individuals pause, look around, pause, or do other things that make them seem less invested. After a bout, they are likely to sit next to one another. There are eight play behaviours.	
		Bite	Initiator bites receiver in a play manner
		Box	Initiator stands on hind legs, using paws to strike opponent in a play manner
		Chase	Initiator chases receiver in a play manner
		Grab/slap/push	Initiator grabs, slaps, or pushes receiver in a play manner
		Pounce	Initiator pounces on receiver in a play manner
		Mount	A mount in the context of play where initiator places its forepaws on the others back and mounts it.
		Wrestle	Initiator and receiver wrestle with each other in a play manner
		Greet	Initiator touches nose of marmot with its nose
	Sit		
		Sit < 1m	Multiple marmots sit within 1 meter of each other but not in body contact
		Sit body contact	Multiple marmots sit in physical contact with each other
	Other		

	Follow	One marmot approaches another and the approached animal moves and this whole interaction occurs three or more successive times
	Forage together	Marmots are together out feeding in an area with food within 1 meter of each other or obviously moving together (not greater than 5 meters apart)
	Allogroom	One marmot grooming another or multiple marmots grooming each other. Often concentrated in places a subject cannot reach (back of neck).

A.2 Chapter 3: Supplement

Supplementary Table A.2.1. Ethogram of social behaviors recorded during marmot observation. Each behavior description is written with a focus on the initiator individual.

Relationship Type	Category	Behavior	Behavior Description
Aggression			
	Fight	Interactions happen quickly and marmots separate quickly afterwards. Interactions more likely to be accompanied by vocalizations (squeaks, yelps, growls, etc.). There are eight types of fight behavior.	
		Bite	Initiator bites receiver in an aggressive manner
		Box	Initiator stands on hind legs, using paws to strike opponent in an aggressive manner
		Chase	Initiator chases receiver in an aggressive manner
		Grab/slap/push	Initiator grabs, slaps, or pushes receiver in an aggressive manner
		Mouth spar	When both initiator and receiver lunge at each other with open mouths in an aggressive manner
		Pounce	Initiator pounces on receiver in an aggressive manner
		Snap/snarl/ hiss	Initiator vocalizes in an aggressive way towards a receiver
		Wrestle	Initiator and receiver wrestle with each other in an aggressive manner
	Displacement		
		Simple Displacement	There is contact between two marmots and one ends up changing locations

		Proximity Displacement	Initiator marmot approaches other within 1 meter and other individual moves.
Affiliative	*Play*	Unlike aggression, play is ‘bouncier’ and individuals change roles repeatedly, regularly changing behaviors. Play can get interrupted where individuals pause, look around, pause, or do other things that make them seem less invested. After a bout, they are likely to sit next to one another. There are eight play behaviors.	
		Bite	Initiator bites receiver in a play manner
		Box	Initiator stands on hind legs, using paws to strike opponent in a play manner
		Chase	Initiator chases receiver in a play manner
		Grab/slap/push	Initiator grabs, slaps, or pushes receiver in a play manner
		Pounce	Initiator pounces on receiver in a play manner
		Mount	A mount in the context of play where initiator places its forepaws on the others back and mounts it.
		Wrestle	Initiator and receiver wrestle with each other in a play manner
		Greet	Initiator touches nose of marmot with its nose
	Sit		
		Sit < 1m	Multiple marmots sit within 1 meter of each other but not in body contact
		Sit body contact	Multiple marmots sit in physical contact with each other

	Other		
		Follow	One marmot approaches another and the approached animal moves and this whole interaction occurs three or more successive times
		Forage together	Marmots are together out feeding in an area with food within 1 meter of each other or obviously moving together (not greater than 5 meters apart)
		Allogroom	One marmot grooming another or multiple marmots grooming each other. Often concentrated in places a subject cannot reach (back of neck).

A.3 Chapter 4: Supplement

Supplementary Table A3.1. Ethogram of social behaviors recorded during marmot observation. Each behavior description is written with a focus on the initiator individual. Adapted from Wey and Blumstein 2010.

Relationship Type	Category	Behavior	Behavior Description
Aggression			
	Fight	Interactions happen quickly and marmots separate quickly afterwards. Interactions more likely to be accompanied by vocalizations (squeaks, yelps, growls, etc.). There are eight types of fight behavior.	
		Bite	Initiator bites receiver in an aggressive manner
		Box	Initiator stands on hind legs, using paws to strike opponent in an aggressive manner
		Chase	Initiator chases receiver in an aggressive manner

		Grab/slap/push	Initiator grabs, slaps, or pushes receiver in an aggressive manner
		Mouth spar	When both initiator and receiver lunge at each other with open mouths in an aggressive manner
		Pounce	Initiator pounces on receiver in an aggressive manner
		Snap/snarl/ hiss	Initiator vocalizes in an aggressive way towards a receiver
		Wrestle	Initiator and receiver wrestle with each other in an aggressive manner
Displacement			
		Simple Displacement	There is contact between two marmots and one ends up changing locations
		Proximity Displacement	Initiator marmot approaches other within 1 meter and other individual moves.
Affiliative			
	Play	Unlike aggression, play is ‘bouncier’ and individuals change roles repeatedly, regularly changing behaviors. Play can get interrupted where individuals pause, look around, pause, or do other things that make them seem less invested. After a bout, they are likely to sit next to one another. There are eight play behaviours.	
		Bite	Initiator bites receiver in a play manner
		Box	Initiator stands on hind legs, using paws to strike opponent in a play manner
		Chase	Initiator chases receiver in a play manner
		Grab/slap/push	Initiator grabs, slaps, or pushes receiver in a play manner
		Pounce	Initiator pounces on receiver in a play manner

	Mount	A mount in the context of play where initiator places its forepaws on the others back and mounts it.
	Wrestle	Initiator and receiver wrestle with each other in a play manner
	Greet	Initiator touches nose of marmot with its nose
Sit		
	Sit < 1m	Multiple marmots sit within 1 meter of each other but not in body contact
	Sit body contact	Multiple marmots sit in physical contact with each other
Other		
	Follow	One marmot approaches another and the approached animal moves and this whole interaction occurs three or more successive times
	Forage together	Marmots are together out feeding in an area with food within 1 meter of each other or obviously moving together (not greater than 5 meters apart)
	Allogroom	One marmot grooming another or multiple marmots grooming each other. Often concentrated in places a subject cannot reach (back of neck).

Supplementary Table A3.2. Datasets and sample sizes for NBDA analyses for location transmission in 2018 and 2019 and both solutions (lid and door) in 2019.

Year	**Interaction type**	**Social Group**	**Number of individuals who interacted with the puzzle box**	**Social group size**
2018	**Location**	Bench	3	11
		Gothictown-Happy Valley	5	8
		Gothictown-Red Rock	5	7
		Picnic	6	15
		Marmot Meadow-Main Talus	9	16
		Marmot Meadow-Aspen	3	16
		Gothictown-Doctors	6	6
		Avalanche	3	4
2019	**Location**	Bench	3	17
		River	9	17
		Gothictown-Happy Valley	11	13
		Gothictown-Red Rock	5	6
		Picnic	8	14

	Marmot Meadow-Main Talus	10	15
	River Annex	7	8
	Boulder	3	3
	North Picnic	5	5
Solution: Lid	Marmot Meadow-Main Talus	5	15
	Picnic	5	14
	North Picnic	2	5
	River Mound	3	17
	Boulder	2	3
	Gothictown-Red Rock	3	6
Solution: Door	Marmot Meadow-Main Talus	2	15
	Picnic	3	14
	Boulder	2	3
	Gothictown-Happy Valley	3	13